

The role of perceptual learning on modality-specific visual attentional effects

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Abstract

Morrone et al. [Morrone, M. C., Denti, V., & Spinelli, D. (2002). Color and luminance contrasts attract independent attention. *Current Biology*, 12, 1134–1137] reported that the detrimental effect on contrast discrimination thresholds of performing a concomitant task is modality specific: performing a secondary luminance task has no effect on colour contrast thresholds, and vice versa. Here we confirm this result with a novel task involving learning of spatial position, and go on to show that it is not specific to the cardinal colour axes: secondary tasks with red-green stimuli impede performance on a blue-yellow task and vice versa. We further show that the attentional effect can be abolished with continued training over 2–4 training days (2–20 training sessions), and that the effect of learning is transferable to new target positions. Given the finding of transference, we discuss the possibility that V4 is a site of plasticity for both stimulus types, and that the separation is due to a luminance-colour separation within this cortical area.

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1. Introduction

Early and influential accounts of visual function, such as those of Wiesel and Hubel (1965a, 1965b) and Marr (1982) conceived of the adult visual system (i.e. the visual cortex) as a hierarchical processing system, hard-wired to extract information about visual objects from the raw retinal image. Research in recent decades, however, has revealed the extent to which *top down attentional effects* modulate the processing of incoming signals in the visual cortex (see Treue, 2001, for review) and even as early in the visual hierarchy as the lateral geniculate (O'Connor, Fukui, Pinsk, & Kastner, 2002), and also the degree of plasticity which is

retained in the mature visual cortex, demonstrated by *perceptual learning* of visual tasks.

There is now an extensive body of literature on perceptual learning, with some evidence for plasticity as early as primary visual cortex, V1 (see Fahle, 2002; Fine & Jacobs, 2002 for reviews). Furthermore, there is evidence that perceptual learning occurs only if the observer is attending to the stimulus to be learned (Ahissar & Hochstein, 1993; but see Watanabe et al., 2002), a finding which is consistent with at least one theoretical account of learning in adult visual cortex (Grossberg, 2003). There has been little investigation, however, of the extent to which attentional effects are modified by learning, though some reported psychophysical and physiological findings are relevant to this question, and will now be discussed.

Ahissar, Laiwand, and Hochstein (2001) have directly addressed the question of how perceptual learning affects attentional processes in early vision. They used a dual task paradigm which required simultaneous

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orientation-discrimination and letter recognition, and measured attentional interference under different training conditions. It is shown that performance in the double tasks could be brought to single task level after training. The authors address the question of whether this improvement is due to increased efficiency of the tasks, such that the fact of a limited attentional resource is no longer significant, or if the improvement is due to an improvement in the higher-order co-ordination of the two tasks. Results showing the effectiveness of prior training in the individual tasks give evidence for the former explanation, consistent with Ahissar and Hochstein (1996) finding that training increases the processing speed of a search stimulus, even under conditions of 100% accuracy at the beginning of training. However, it was found that even after successful training, performance in both tasks would fall if one of the tasks was made more difficult. This suggests that training does not lead to full automaticity of the tasks, and that processing of the dual stimulus is still somehow limited by a fixed attentional resource.

Gilbert, Ito, Kapadia, and Westheimer (2000) report a study on surround effects in V1 involving human psychophysics and physiological and behavioural experiments on primates. They show that the response facilitation caused by a collinear flanker outside the classical receptive field is initially greater under a condition of distributed spatial attention, than in the case when attention is focussed on the receptive field. Monkeys were then overtrained in the distributed attention experiment, and it was found that the facilitation was much reduced, and that the responses came to be equivalent to those in the focussed attention condition. It is as if, the authors observe, the monkeys learn to focus their attention in a divided way. The learning was found to transfer to an experiment involving new spatial positions, but not to an experiment involving distributed attention over twice as many loci.

This paper follows on from the work of Morrone, Denti, and Spinelli (2002, 2004) that gave evidence for the existence of separate attentional resources for colour and luminance stimuli, and shows how such attentional effects can themselves be altered by training, presumably by plasticity of the visual system.

Morrone et al. (2002, 2004) presented peripheral luminance or equiluminant gratings simultaneously with central visual search stimuli (either luminance contrast, or equiluminant colour contrast). They measured the contrast discrimination thresholds for the gratings in a single task condition, in which the observer was asked to ignore the central stimulus, and double task condition, in which the observer had to perform the visual search as well as the peripheral contrast discrimination. They reported attentional interference in the double task condition, that is, a consistent increase in threshold when contrast discrimination was performed at the same time as the visual search. But this effect occurred only when the central and peripheral stimuli were of the same contrast modality: processing of a coloured central stimulus did not impair discrimination of black and white gratings, and vice versa.

These authors propose that the processing of a central stimulus causes a selective reduction of the gain of the neuronal response to a peripheral stimulus of the same contrast modality. It is suggested that there are separate, limited attentional resources for luminance and colour stimuli, but the question of whether there are separate attentional resources for differently coloured stimuli was left open, since the only coloured stimuli used were modulated along the red-green cardinal axis. It was not suggested that the effect caused by the central task may alter or diminish with training, it being assumed that the attentional resources involved have a fixed capacity, and that the attentional load of the central task does not change with training. These assumptions are called into question by the findings of this paper. The first experiment shows that the large attentional effect (up to 0.5 log-unit difference in discrimination threshold) can be abolished with overtraining of the discrimination and search double task. The second experiment uses a new central task which involves learning to recognise the position of a small fixed luminance or colour circle in a field of random circles of the same contrast modality. This experiment was designed to allow for further investigation of time-course, duration and transfer of perceptual learning, and its effects on attentional modulation, and one of the motivations for studying learning in this experiment is that issues such as the transfer of learning help to shed light on the anatomical locus of the attentional effect. It was found that the attentional effect was specific to colour or luminance stimuli, but not to the specific colour of the stimuli, suggesting that the attentional separation is indeed specific for colour versus luminance. Again, it was found that the effect could be abolished with overtraining. Furthermore, the finding of transfer of learning across spatial position implicates an extrastriate origin of the effect.

2. Methods

2.1. Observers

There were four observers, all had normal or corrected to normal acuity, the three observers who participated in the colour conditions had normal colour vision. Observers MC and MCM are authors. AT and CB were naïve to the aims of the experiment. MC participated in all conditions of both experiments and in the transfer task, MCM participated in Experiment 2: luminance condition and red-green condition, AT participated in Experiment 1: luminance condition, and CB participated in Experiment 2: blue-yellow condition and in the transfer task.

2.2. Equipment

Stimuli were presented on a Barco *calibrator* monitor whose gun CIE coordinates were, for red $x=0.618$, $y=0.342$, $Y=8.77$ cd/m²; for green $x=0.292$, $y=0.592$, $Y=25.2$ cd/m² and for blue $x=0.142$, $y=0.071$, $Y=2.59$ cd/m². The luminance of the mean grey was 37 cd/m².

For each observer equiluminance was measured along the two cardinal colour axes of the Derrington, Krauskopf, and Lennie (1984) colour space, that is, for constant S-cone activity (red-green modulated) or for constant L-M cone activity (blue-yellow modulated). Two separate procedures were used: evaluation of minimum flicker of a circular patch (5 deg diameter) of 1 c/deg sinusoidal grating counterphasing at 15 Hz;

and by measuring detection thresholds for the grating patch and choosing the colour ratio to yield minimum sensitivity. The equiluminance measurements for the three different observers were not noticeably different, so the colour settings were kept the same for all observers throughout the experiment. For red-green stimuli of maximum contrast (0 log-units), the green was modulated from 9.52 to 18.5 cd/m². For blue-yellow stimuli, for maximum modulation of blue, the green gun modulated from 11.8 to 16.2 cd/m² and the red gun in antiphase to the green from 4.41 to 5.33 cd/m².

2.3. Stimuli

The peripheral stimuli were horizontal sinusoidal gratings presented above and below the central stimulus. The gratings measured 39.5 deg across (the full width of the screen) by 9.0 deg height. The gratings were modulated along either of the two cardinal axes of the isoluminance plane of the Derrington et al. (1984) colour space, or luminance modulated, along the axis perpendicular to the isoluminance plane in this colour space. The spatial frequency of the gratings was always 1 cycle/deg. The gratings were presented 2.5 deg from the fixation point, central enough to keep the coloured stimuli within the cone-rich part of the central visual field. The phase of the gratings was randomised from trial to trial to prevent adaptational effects.

On each trial one of the gratings had a higher contrast than the fixed pedestal contrast, and the observer's task was to identify which. The values of pedestal contrast were chosen to be in the range giving maximum facilitation with respect to absolute detection threshold (i.e. in the dip of the dipper function), as this contrast range at which Morrone et al. (2002, 2004) report the greatest attentional effect. The adaptive QUEST (Watson & Pelli, 1983) procedure varied the contrast so that it remained near threshold on every trial. Contrast discrimination thresholds were evaluated by fitting a cumulative Gaussian function to the percentage of correct responses. Standard errors of the thresholds were estimated by a bootstrapping routine.

The central stimulus was a field of 18 small circles subtending 0.4 × 0.4 deg (6 × 6 pixels). The circles appeared at random positions within a 6 deg by 4 deg rectangle in the centre of the screen. As with the peripheral gratings, the colour setting of circles was either red-green, blue-yellow, or black and white. In each case, the majority of the circles would be of one colour/luminance polarity, with one or two circles of the opposite polarity. The observer was asked to respond to the central stimulus only in the double task conditions of both Experiments 1 and 2. In these conditions, the peripheral discrimination data were discarded if the central task response was incorrect.

Both central and peripheral stimuli were presented on every trial, appearing simultaneously for 50 ms. A white fixation point appeared in the centre of the screen throughout the experiment, the observer being requested to fixate, even when responding to the peripheral stimuli. The viewing distance was 57 cm.

Contrast values for the stimuli given below are in log units of attenuation from 100% contrast. In the case of the equiluminant stimuli, contrast attenuation given is for the maximally modulated gun (the red gun in the case of the RG stimuli, and the blue gun in the case of BY stimuli). See Fig. 1 for an illustration of the stimulus configuration.

2.4. Experiment 1: Effect of learning on divided attention in a pop out task

This experiment involved a series of repetitions of one of the experiments reported by Morrone et al., 2002, 2004, in order to track the effect of perceptual learning on the spatial attention effect reported by these authors. The central task was a simple pop-out visual search: the target circle of opposite colour/luminance polarity would appear on 50% of the trials, and the observer was asked to report whether or not the target had appeared. Observer MC performed the experiment in both RG and luminance conditions, AT only in the luminance condition.

The task was difficult (attentionally demanding) because of the low contrast of the central stimuli (luminance stimuli at 1.2–1.3 log-units, red-

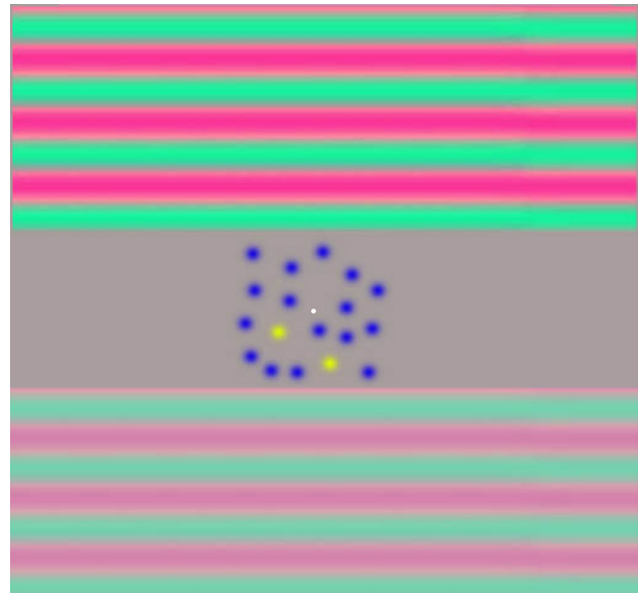


Fig. 1. An illustration of the stimulus configuration, not drawn exactly to scale (actual gratings were 39.5 deg × 9 deg, 1 cycle per deg; circles 0.4 deg diameter). Incongruent colour configuration (RG peripheral gratings, BY central task). Actual colour stimuli were equiluminant (not as illustrated), falling along the cardinal axes of the Derrington et al. (1984) colour space (i.e. RG along L-M axis, BY along S-LM axis). The stimulus was the same for both Experiments 1 and 2 (see below), except that in Experiment 1 only one opposite colour dot would appear, and in Experiment 2 two would appear, as depicted. In both experiments, central stimuli would be at a lower contrast than illustrated here. (For interpretation of colour mentioned in this figure the reader is referred to the web version of the article.)

green stimuli at 0.8 log-units). Peripheral discrimination thresholds were measured in the single-task, in which the central stimulus appeared but the observer responded only to the peripheral stimulus, and in the double task, in which the observer was asked to perform the visual search as well as the peripheral discrimination. Pedestal contrast was facilitating (luminance at 1.7 log-units (MC) or 2.5 log-units (AT); RG at 1 log-unit).

1–2 training sessions of 60 trials were conducted on 2–4 consecutive days (up to 360 trials total), until the attentional effect was effectively eliminated. Only the congruent condition was tested, that is, the central and peripheral stimuli were either *both* red-green equiluminant or *both* luminance modulated. MC learnt the RG and luminance conditions separately, on different days (RG training was performed after luminance training had been completed).

2.5. Experiment 2: Effect of learning on divided attention in a target localisation task

In further experiments, blue-yellow equiluminant stimuli were used in the centre and periphery, as well as the previously described red-green and black and white types. As in Experiment 1, the peripheral task was contrast discrimination of luminance or equiluminant gratings which appeared close to the central stimulus. The pedestal contrast was always in the facilitating range, 1.15 log-units for the chromatic gratings and 2–2.5 log-units for the luminance gratings.

The appearance of the central stimulus was the same as in Experiment 1, with the difference that there were now always *two* circles with the opposite colour/luminance polarity from the other fourteen. The positions of the circles were always randomised, except for the position of *one* of the two opposite-polarity circles, which was fixed on 50% of the trials. Now, in the double-task experiment, the observer was required to perform an attentionally demanding learning task. On each trial, the observer had to report whether or not the circle with the fixed position had appeared

amongst the random circles, responding positively or negatively, before making the response to the peripheral contrast discrimination task. In advance of the experiment, the observer was not told the position of the fixed circle. Instead, the observer had to deduce the fixed circle position from observation of a few trials. This was always achieved within the first experimental run of 32 trials.

In order to keep the difficulty of the central task around at 80%, pilot tests were run in order to find this “threshold” contrast level for each observer. Thus the contrasts of the central circles were different for different observers: for MC the luminance contrast was 1.3 log-units, the red green contrast 0.6 log-units and the blue yellow contrast 0.4 log-units; for MCM the luminance contrast was 1.3 log-units and the red-green and blue-yellow contrast 0.2 log-units; for CB the red-green contrast was at 0.2 log-units and the blue-yellow contrast 0.1 log-units. These differences in central stimulus contrast for the different observers were found to make no appreciable difference to the results.

In an experimental session, the subject would perform a series of QUEST runs of both the single and the double task, and using two of the three different colour settings for the central stimulus, but with a fixed colour for the peripheral gratings. For example, in one session the discrimination thresholds for red-green gratings would be measured with a red-green (congruent) and a blue-yellow (incongruent) central stimulus, in both the single and double task conditions. Thus, congruent and incongruent conditions were learned simultaneously. Up to four practise sessions of 60 trials were conducted over 3–4 days, until the attentional effect was eliminated.

3. Results

3.1. Experiment 1: Effect of learning on divided attention

The first experiment was a repetition of the contrast discrimination/visual search double task paradigm of Morrone et al. (2002, 2004), the difference being that training sessions of 60 sessions were repeated over 2–4 consecutive days, in order to study the effect of perceptual learning.

Fig. 2 shows contrast discrimination thresholds in the single and double task conditions for two observers for luminance stimuli (a and b) and for one observer for red-green equiluminant stimuli (c). In both cases, there is a large difference in the threshold for the double task, compared to the single task, on the first day of training. As reported by Morrone et al. (2002, 2004), it seems that in the double task, the focus of attention on the central visual search, makes it harder for the observer to compare the contrasts of the peripheral gratings, thus resulting in an increase in the discrimination thresholds. However, by the second day of training for MC, and after the third day for training for AT (at least 200 trials), the attentional effect is shown to diminish, with equal thresholds in the single and double task conditions in some of the conditions. It was not the case that the observer has simply stopped paying attention to the central task, as performance rates were checked and found to stay consistently around 80% correct (remember also that responses to the peripheral discrimination were not counted for trials in which the observer gave an incorrect response to the central task). Thus it seems that observer learns to perform the visual search more efficiently, so that the extra attentional load of the double task becomes negligible. This is consistent with the observation that the threshold for the single task is approximately stable across the different days of

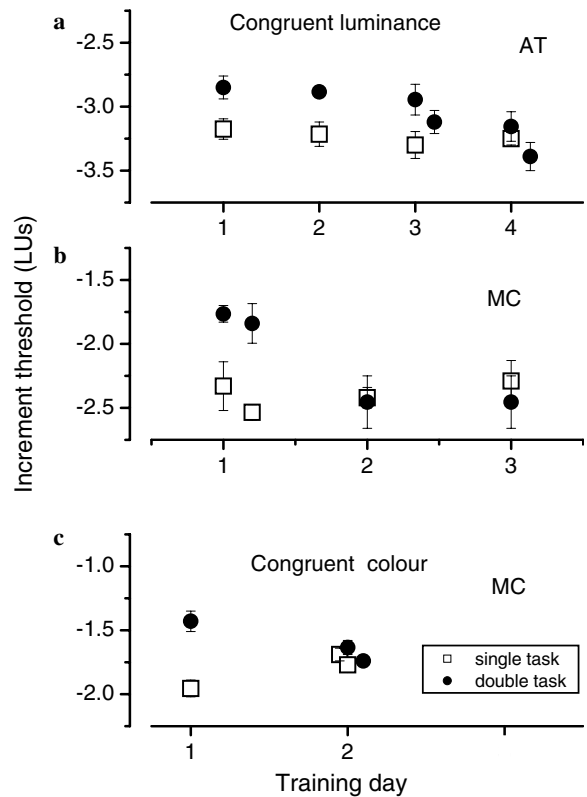


Fig. 2. Results of Experiment 1, showing the effect of learning on divided attention in the pop-out search task of Morrone et al. (2002, 2004). (a) Observer AT, congruent luminance stimuli; (b) MC, congruent luminance stimuli, presented eccentrically; (c) MC, congruent RG stimuli. For both observers and in both conditions, the initial separation between the double task (closed circles) and single task (open squares) thresholds disappears by the end of training.

the experiment, while the discrimination threshold in the double task drops down to this level. So it is not the case that observers' contrast discrimination improves overall.

3.2. Experiment 2: Selective attentional interference for luminance and equiluminant stimuli in a new dual task

The central and peripheral stimulus configuration in the second experiment was the same as in the first experiment, but the central task was no longer simple visual search; instead, it required conscious learning of the previously unknown position of a fixed circle which had a luminance/colour polarity different from that of all but one of the other, randomly positioned circles. Learning was arranged in sessions of 60 presentations of up to four possible combinations of *experiment type* (single task versus double task) and *stimulus type* (congruent central stimulus versus incongruent central stimulus, depending on whether or not the central stimulus was on the same luminance/colour axis as the peripheral stimulus). So single and double, congruent and incongruent tasks were practised simultaneously.

The observers performed up to five sessions on any one day, and learning was continued for up to four days, as long as it took for the attentional effect to be attenuated.

Peripheral discrimination thresholds in the double and single tasks are plotted against day and session, in order to show the rate at which the attentional effect of the central task diminishes with practice. Each data point shows the threshold measured for each session in the double task (closed circles). Where there are fewer data points for the single task (open squares), single task results for all sessions of that day have been pooled, since single task thresholds were consistently stable for all observers.

Figs. 3a and b show data for the congruent task in which the peripheral stimuli were low contrast luminance gratings and the central stimulus was a set of luminance circles. Note the large difference between single task and double task thresholds at the start of training. The size of this attentional effect (around 0.5 log-units) is the same as that reported by Morrone et al. (2002, 2004) and measured in Experiment 1, suggesting that the attentional load (and therefore the attentional effect) due to the new learning task is equivalent to that due to the simple visual search task. The time course of training is also similar to that of the visual search, as shown in the results of the Experiment 1. It

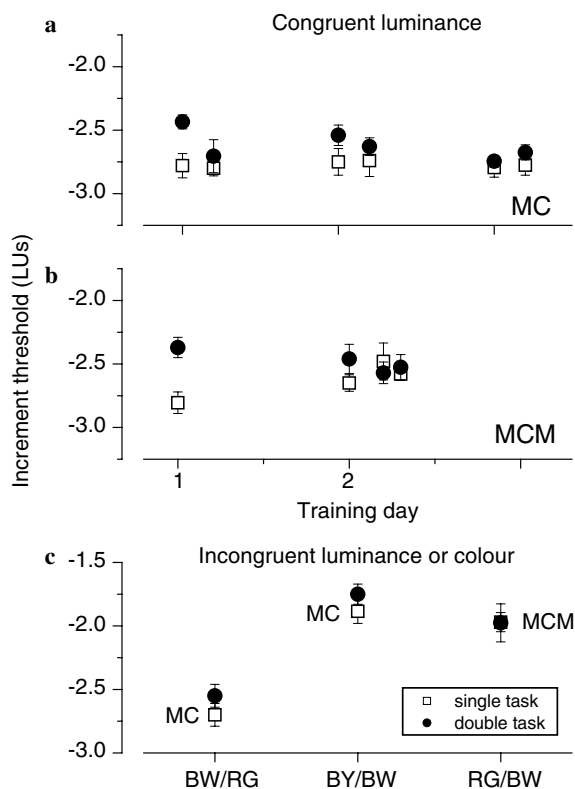


Fig. 3. Results of Experiment 2, showing the effect of learning on divided attention in a target localisation task for congruent luminance stimuli and incongruent chromatic and achromatic stimuli. (a) Observer MC, congruent luminance stimuli; (b) MCM, congruent luminance stimuli; (c) MC, incongruent luminance peripheral and RG central stimuli; MC incongruent BY peripheral and luminance central stimuli; MCM, incongruent RG peripheral and luminance central stimuli. (a) and (b) In the congruent luminance condition the attentional effect for this new experiment also disappears with training. (c) As in the previous results of Morrone et al. (2002, 2004), there is no initial attentional effect for incongruent RG-luminance stimuli.

therefore seems that the two experiments (i.e. pop-out search and position learning) are using the same attentional mechanism. This idea is supported by Figs. 3c, which shows that the use of an incongruent red-green isoluminant stimulus has little effect on discrimination thresholds for the luminance gratings and, equivalently, that the use of a luminance-modulated central stimulus does not affect the discrimination thresholds of either red-green or blue-yellow isoluminant peripheral gratings. It should be pointed out that these data were collected on the first day of training along with the congruent data, and so the lack of the effect cannot be explained by prior learning of the congruent task. Thus it may be concluded that the attentional interference caused by the new central task is specific to the processing of luminance or chromatic peripheral stimuli, just as Morrone et al. (2002, 2004) showed that processing of a luminance or equiluminant central pop-out stimuli caused an attentional effect specific to the stimulus type.

3.3. Learning and attentional interference between equiluminant stimuli

The aim of these experiments was to find out whether the attentional mechanism previously shown to be specific to the processing of coloured versus luminance stimuli is also specific to the particular colour of equiluminant stimulus. That is, whether attentional interference will occur between stimuli that lie on perpendicular colour axes, here the cardinal axes of the Derrington et al. (1984) colour space. Thus in these experiments, the congruent condition used central and peripheral stimuli modulated along the same colour axis, and in the incongruent condition the central and peripheral stimuli were modulated along perpendicular colour axes.

Fig. 4 shows the learning curves of observers CB and MCM for discrimination of 1.15 log-unit pedestal RG and BY gratings in both congruent and incongruent conditions (where, again, the congruent and incongruent data were collected simultaneously). Note that both observers show an attentional effect in the first sessions, in both the congruent and incongruent conditions, showing that this effect is not specific to the cardinal colour axes. The results suggest that even though the magnitude of the attentional effect is the same at the start of training for both the congruent and incongruent conditions, the attentional effect is more persistent in the incongruent colour condition. For MCM, thresholds converged after the second day of training (after 180 trials) in the congruent condition, and on the fourth day of training (after more than 200 trials) in the incongruent condition. For CB the effect was overcome in both the congruent and incongruent colour conditions on the third training day, but five additional training sessions were required for the incongruent condition on those days. So, it appears that not only is the attentional interference not specific to the colour axis, but that the interference is less easy to overcome by training when the central and peripheral stimuli fall on different colour axes. This could be, for instance, because there is a certain facilitatory effect that occurs between congruent stimuli

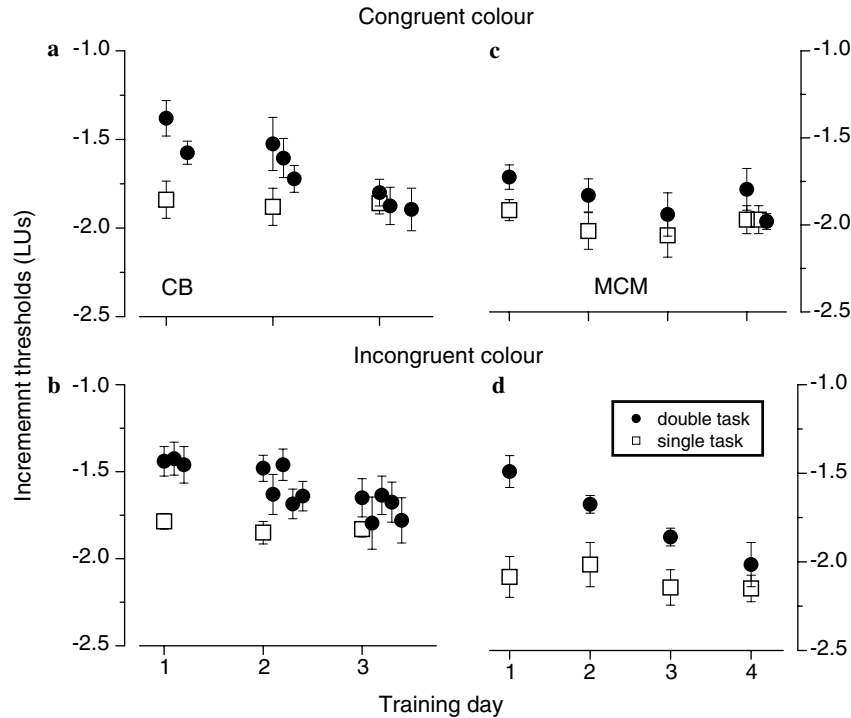


Fig. 4. Results of Experiment 2 showing the effect of learning on divided attention in a target localisation task for congruent and incongruent RG and BY stimuli. (a) CB, congruent BY stimuli; (b) CB, incongruent BY peripheral and RG central stimuli; (c) MCM, congruent RG stimuli; (d) MCM, incongruent RG peripheral and BY central stimuli. (b) and (d) demonstrate the attentional effect for incongruent RG-BY stimuli. The small initial separation in (c) seems to be due to an unusually high single task threshold recorded in this session.

(Saenz, Buracas, & Boynton, 2003). Note that this difference between the congruent and incongruent results cannot be explained by the possibility of it being intrinsically more difficult to perform either the discrimination of the localisation task along one of the colour axes, as the effect was equally strong when either the peripheral or the central stimuli were blue-yellow or red-green.

Fig. 5 shows further data, the learning curves of MC in the incongruent condition for Experiment 2. This observer had undertaken large number of pilot tests in during the development of the experiment and so was already more practised than the other observers. For this reason it seems that learning occurred more rapidly during the actual data collection, than it did for the naïve or less trained observers (see next section on transfer of learning).

3.4. Transfer of learning

This set of experiments was carried out in order to see if the effects of learning a particular circle position persisted after the training period, and if the learning would transfer to new circle positions. On the day following the completion of training with RG and BY stimuli, experiments were carried out by CB and MC in which they had to respond to new fixed circle positions located in another part of the central field relative to the fixation point but using the same stimulus settings in all other respects (e.g. same contrasts). The new circle positions were always at about the same distance from the fixation point as before, so that the difficulty of the task

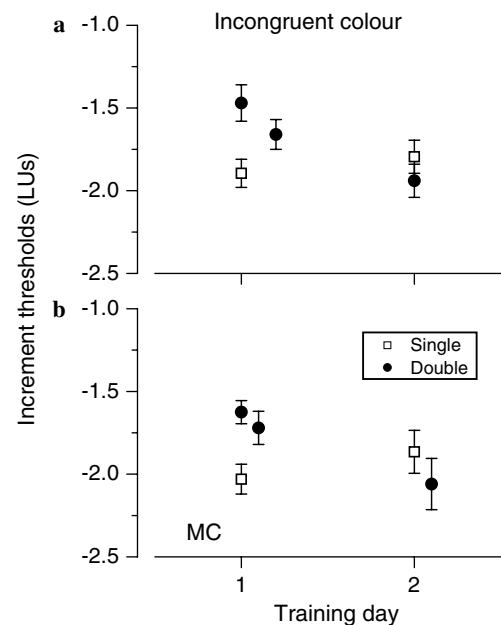


Fig. 5. Further results for Experiment 2: observer MC incongruent RG and BY stimuli. (a) MC, incongruent BY peripheral and RG central stimuli; (b) MC, incongruent RG peripheral and BY central stimuli.

did not change. Fig. 6 shows discrimination thresholds for coloured gratings with coloured central stimuli which had new fixed circle positions. CB's results show complete transference of learning, with no evidence of an attentional effect for either the congruent or incongruent central stimulus

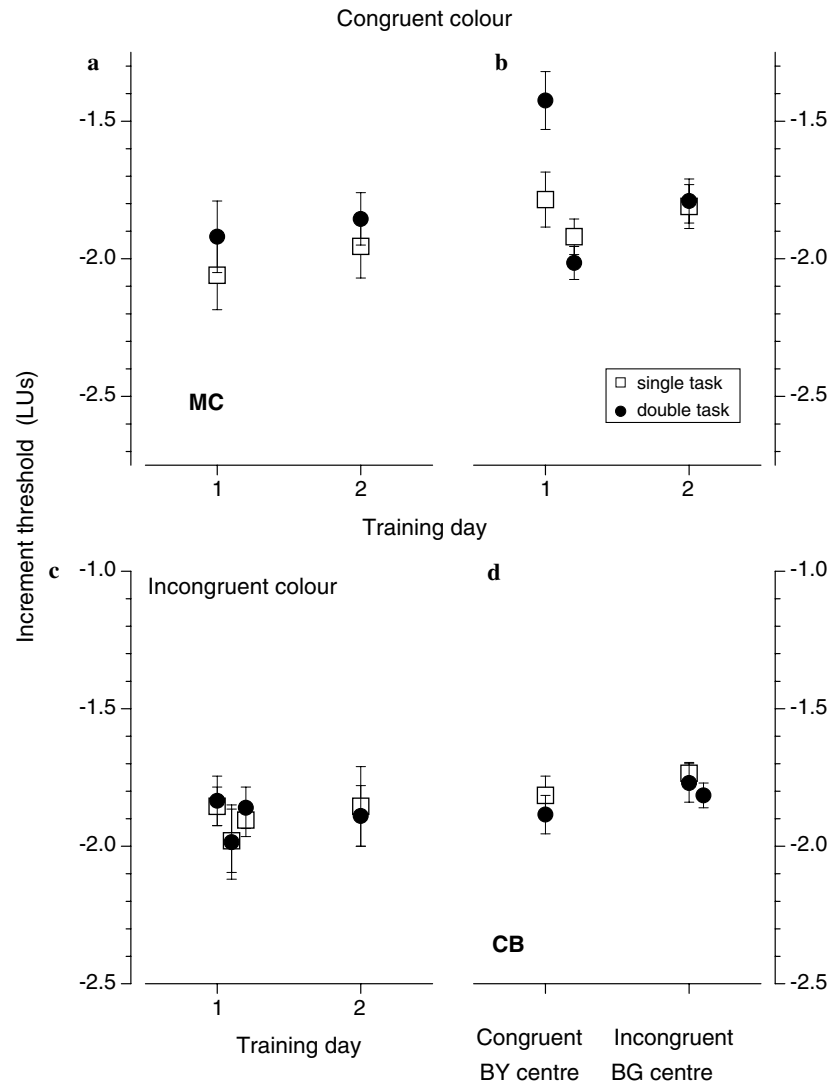


Fig. 6. Results of Experiment 2 using a novel central target position, in order to show transference of learning. (a) Observer MC, congruent RG stimuli; (b) observer MC, congruent BY stimuli; (c) MC, incongruent BY peripheral and RG central stimuli; (d) CB, congruent BY stimuli; incongruent BY peripheral and RG central stimuli.

(Fig. 6d). Although one of MC's data points shows evidence of an attentional effect for the new congruent BY task (Fig. 6b), this point may well be an anomaly, since the effect vanishes in the next session, a much faster elimination of the effect than seen on any of the original experiments. It seems reasonable to conclude that for both observers tested learning is fully transferable across spatial position. This is an important finding bearing on the question of the possible location of plasticity in the visual brain.

4. Discussion

The work presented in this paper is a continuation of the investigation of Morrone et al. (2002, 2004) on the existence of separate attentional resources for luminance and colour mechanisms. The main finding is the result that the sort of attentional effects previously reported can be abolished with training; thus the amount attentional interference

caused by a distracter task is not only a function of its intrinsic attentional load, but also the observer's state of training. The experiments provided no evidence for the existence of separate attentional resources for different colour channels (i.e. the red-green and blue-yellow cardinal axes). All of these data raise the question of the physiological basis and critical anatomical locus for perception, attention and learning involved in the experiments.

4.1. What is learnt in double tasks: higher order strategy or improved low level processing?

The demonstration of improved performance with training in a dual task experiment leads to the important question of where in the series of processing stages the improvement is most likely to have occurred. Does the improvement reflect increased proficiency in the higher-order co-ordination of the two tasks, or is the attentional

effect decreased because of an increased efficiency in the low-level processing of the individual stimuli, reducing their attentional load?

A number of observations bear against the higher-order co-ordination hypothesis. One obvious point is that one subject (MC), who performed the second experiment having previously learnt the first experiment, showed as large an attentional effect at the start of training in Experiment 2 as observers with no previous experience at performing dual-tasks. Similarly, MCM had experience in performing the task similar to Experiment 1 (Morrone et al., 2002, 2004) prior to learning Experiment 2, and this did not affect the size of the attentional cost measured in Experiment 2. Also, MC trained in the RG congruent task in Experiment 1 after having previously learnt the luminance congruent task, and again had a strong initial attentional effect. However, since these significant sequences of experiments arose coincidentally, not being part of the actual experimental design, they would bear confirmation with one or more other observers in a directly controlled series of tests.

A further reason for attributing learning to a sensory rather than motor area plasticity is that it is reasonable to assume that the site of greatest plasticity is the same as the site implicated in the attentional effect. (cf. Fuster (1995) for argument that the greatest plasticity occurs at the site where the stimulus is normally decoded.) Since this attentional effect is specific for colour or luminance, its locus must be a visual area, rather than a higher-order coordination area.

4.2. Location of the effect in the visual pathway

Given the above evidence for a sensory (rather than a motor or cognitive) brain area as the significant locus of plasticity, it is now natural to ask where in the visual pathway this might occur. Since all of the tasks, including those of Experiment 2, involve recognition of stimulus properties (contrast, colour or position), and do not require stimulus-observer motor interactions, it seems reasonable to assume that the relevant processing takes place in the “ventral” stream which runs from specific channels in V1 through to the infero-temporal cortex (IT).

However, the strong luminance-colour separation of the effects reported in the current experiments, and also those of Morrone et al. (2002, 2004) could be taken for evidence that the separation is between dorsal and ventral streams, with the luminance stimuli being processed dorsally and the equiluminant stimuli being processed ventrally. Indeed, this is the explanation put forward by Morrone et al. (2002, 2004) of the modality-specificity of the attentional effect, and strong attentional effects have been reported in fMRI studies of early visual areas, LGN (O’Connor et al., 2002) and V1 (Ghandi, Heeger, & Boynton, 1999; Watanabe et al., 1998).

Just as there have been reports of attentional effects from early pre-cortical areas through to extrastriate areas, physiologists have reported plasticity at various stages of the visual cortex: V1 (Crist, Li, & Gilbert, 2001; Schoups, A, Vogels, Qian, & Orban, 2001) V1 and V2 (Ghose et al.) and

V4 (Yang & Maunsell, 2004). So to address the question of the locus of the effects reported in this paper, the most relevant finding is that learning can be transferred from one location to another for stimuli of the same modality within the 6deg by 4deg window of the central stimulus (see Fig. 6). Since individual V1 receptive fields are much smaller than this window, this transference would rule out V1 as a locus of plasticity. Consistent with this is the main finding of experiment 1 (Fig. 2), that learning takes place for a task in which the target may appear at any random location within the central window. And indeed, the finding that the time course of learning is the same in Experiments 1 and 2, a parsimonious explanation is that learning may take place at the same anatomical locus for the two different central tasks.

This might be contrasted, however, with the findings of Karni and Sagi (1991). These authors measure performance in a pop-out orientation discrimination (at a fixed location) as a function of mask stimulus-onset-asynchrony (SOA) over a number of training sessions. Karni and Sagi report no transference to untrained locations, and little transference between the two eyes in the monocular presentation condition, from which they conclude that learning of this pop-out task is due to plasticity in primary visual cortex (V1), where neurons have small receptive fields of one degree or less, and do not compute complex stimulus properties. However, this result is controversial for Schoups and Orban (1996) did not replicate the finding of ocular specificity. Along with Wolfe and Franzel (1988) and He and Nakayama (1994), Schoups and Orban (1996) argue that the weight of evidence lies in favour of an extrastriate locus of plasticity for pop-out tasks, of which the simple search of experiment 1 would be an example. Also, Ahissar and Hochstein (1996) report a number of generalisations of learning: transfer from trained to untrained eye, to “mirror image” and expanded stimuli, and in space to homologous positions across the midline of the visual field, though not to nearby locations. They suggest that the site of this early perceptual learning is V2–V4, areas which receive substantial input from V1.

So, the extent of transfer in Experiment 2 appears to rule out V1 as a critical site of plasticity. A number of observed features of monkey extrastriate physiology are consistent with our psychophysical findings, and implicate areas such as V4 as important to the specific learning and attentional effects of the sort we report above. Physiological studies have reported attentional modulation of the responses of V4 neurons by spatial attention (Connor, Gallant, Preddie, & Van Essen, 1996, 1997; Mountcastle, Motter, Steinmetz, & Sestokas, 1987) and by feature attention (Chelazzi, Miller, Duncan, & Desimone, 2001; Haenny, Maunsell, & Schiller, 1988; Maunsell, Sclar, Nealey, & DePriest, 1991; Motter, 1994a, 1994b; Ogawa & Komatsu, 2004), and both spatial and attentional modulations for the same neurons (McAdams & Maunsell, 2000). Pinsk, Doniger, and Kastner’s (2004) fMRI study on human observers has reported attentional effects in the homologue of V4. Of particular

relevance to the current experiments, monkeys (De Weerd, Peralta, Desimone, & Ungerleider, 1999) and humans (Galant, Shoup, & Mazer, 2000) with V4 lesions have been reported to have shown performance deficits in discrimination tasks in the presence, but not in the absence of distracter stimuli.

Although, as noted above, correlates of perceptual learning have been found in various cortical areas, Yang and Maunsell (2004) argue that their reported effect in monkey V4 is greater than the modifications reported by equivalent studies on earlier visual areas (Ghose, Yang, & Maunsell, 2002 on V1 and V2; Crist et al., 2001; Schoups et al., 2001 on V1) and argue that V4 might be the critical locus of plasticity for many of the reported cases of early perceptual learning. They point out that V4 is early enough to be responsive to the simple stimuli used in experiments on early perceptual learning (including the luminance and colour gratings and small circles of the experiments reported in this paper), unlike IT which, although known to be highly plastic (Sigala & Logothetis, 2002), appears to be specialised for complex stimuli such as hands and faces.

It must be emphasised, however, that the comparison of human psychophysical results and the known physiology of monkey V4 cannot be made with a satisfactory degree of precision because the question of the homologue of monkey V4 is a point of extreme controversy in the literature (see Tootell & Hadjikhani, 2001; Tootell, Nelissen, Vanduffel, & Orban, 2004), though the consensus is now that V4 is not a specialised colour area (Tootell et al., 2004). For example, it seems that posterior inferotemporal cortex, the area of human cortex implicated in achromatopsia (Heywood, Gaffan, & Cowey, 1995), is not equivalent to monkey V4 because lesions in this area have not been found to cause impairment in wavelength discrimination (Schiller, 1993; Walsh, Carden, Butler, & Kulikowski, 1993). The most that one can say with confidence is that the learning and attentional effects reported here implicate an extrastriate area before IT, which may have some of the physiological properties reported in monkey V4.

4.3. *Separate attention for luminance and colour, but not for the cardinal colour axes*

The main finding of Morrone et al. (2002, 2004), confirmed by the present study, is that there are separate attentional resources for the processing of chromatic and achromatic stimuli. This separation suggested to these authors that a critical processing area was in the early visual cortex, or was perhaps even pre-cortical, where colour and luminance streams are thought to be clearly separated (that is, in the M and P channels of the lateral geniculate). But since, as discussed in the previous section, the nature of the plasticity observed appears to be more consistent with an extrastriate locus, it should be asked whether the extrastriate explanation is consistent with the colour-luminance attentional separation.

First, it should be pointed out that the new finding that attention is not separate for the two cardinal colour axes is, perhaps, evidence *against* an early critical locus. This is because there is some evidence that S-cone outputs are processed separately from the L- and M-cone outputs in a third K-pathway (Martin, White, Goodchild, Wilder, & Sefton, 1997; White, Wilder, Goodchild, Sefton, & Martin, 1998) in the LGN, which has specific V1 input layers. Thus, on the hypothesis that attentional separation is for stimulus characteristics processed by different channels, the anatomy of early vision might predict an attentional separation between the cardinal colour axes.

On the other hand, there is some evidence for continued separation of achromatic and chromatic information in extrastriate cortex, without a separation for the cardinal colour axes (Livingstone & Hubel, 1988; but see Sincich & Horton, 2005). Furthermore, Xiao, Zych, and Felleman (1999) report that the thin stripes and interstripes of V2 have selective projections to areas in monkey V4, where again there is evidence for retained functional separation of areas containing a majority of either colour selective or orientation selective cells, though there is also evidence for convergence of these substreams in V4, for example, Ghose and Ts'o (1997) report the existence of large intervening areas between these substreams in which the neurons have heterogeneous receptive field properties. Given evidence for both separation and convergence of chromatic and achromatic information in extrastriate cortex, it is interesting here to consider Grossberg (2003) argument that separate but complimentary (and therefore interconnected) modules are necessary in higher vision for overcoming uncertainty constraints on what visual problems can be solved. For example, it might be physically impossible to solve the problem of colour constancy without a loss of information about detailed form. Thus, there will be a "colour" module to solve this problem which is interlinked with a form module which retains the information that the colour module sacrifices.

Xiao et al. (1999) speculate that the picture of V4 organisation that they present, "allows for the switching of attention between colour and form modules for rapid searching of objects based on one feature." Even so, it is not necessarily the case that these substreams are consistent with the psychophysical attentional separation. For one thing, they note a separation between colour and *form*, whereas the psychophysical separation under consideration is for stimuli of the same form that are modulated in either colour or luminance contrast. Still, it could be the case that the colour stimulus is preferentially processed (i.e. attention is focussed) by the colour and not the form substream, since the task involves colour pop-out and does not require detailed processing of shape. More difficult to reconcile with the substreams hypothesis is the finding of Motter (1994a), that three-quarters of V4 neurons recorded were responsive to either colour or luminance, depending on which feature the animal was required to attend to. If this result is indeed representative of the majority of neurons in

V4, it is impossible to talk of fixed processing streams in this area. However, it may be that the reported attentional separation may not require an anatomical separation, in which the cortex contains neurons responsive exclusively either to colour or to luminance. The substrate of the separation may just be some banks of neurons responsive both to colour and luminance (as most visual cortical neurons appear to be) but which respond more vigorously to one or the other stimulus type.

4.4. Feature versus spatial attention

The results of these studies suggest the mediation of an attentional mechanism that is neither purely spatial or feature-based, but involves both types of attention. Or in other words, these experiments offer no basis for a clear distinction between spatial and feature attention. The attentional effect of the first experiment must be due to a focussing of spatial attention in the centre, at the cost of processing in the periphery. This central visual search task, however, seems at the start of learning to have an attentional load that relies on feature-based attention, since what is required (and what is improved by training) is the ability to detect a particular object at any location within the field of distracters. Furthermore, in the second experiment, observers are trained to detect a target fixed at a particular location, a task which could, in principle, involve learning only of a spatially localised spotlight. However, the transfer of learning to different spatial locations demonstrates that the attentional load that is overcome with training is not purely spatial, but involves some feature based (and task/strategy based) components. This characteristic of the task might again be consistent with a V4 hypothesis, since Adams and Maunsell (2000) report the existence of neurons in V4 that are modulated by both spatial and feature attention, in both colour and luminance conditions.

4.5. The importance of learning effects in the study of attention

It is interesting to consider, finally, the significance of the result that a seemingly fixed limit on attentional resources can be overcome with intensive training. There is a tendency to conceive of attention as a rigid, structural mechanism, or a finite neural resource, rather than a dynamic capacity of the brain which may adapt to challenges posed by divided attention tasks such as ours. However, the clear result presented in this paper that attentional costs set by distracter tasks may be overcome means that studies which measure the attentional load of tasks should, in the future, take into account the extent of observers' training. For example, the discrepancy between Braun and Julesz (1998) and Sagi and Julesz (1985) over the attentional cost of various detection and discrimination may also have an origin in a difference in the amount of training undertaken by observers in the different experiments. In another dual task experiment, Lee, Koch, and Braun (1999) reported some

learning effect after 234–240 trials. It is worth asking if double task would possibly reach single task performance after even more trials (overtraining), since in the experiments reported above, the attentional effect was normally only abolished after more than 250 practise trials.

5. Conclusions

Using a slightly modified distracter task (Experiment 2), we have reported that the modality specific attentional effect reported by Morrone et al. (2002, 2004) is not specific to cardinal colour axis, and moreover, that this attentional effect disappears with training. Learning was also shown for the original distracter task (Experiment 1). The pattern of perceptual learning perhaps suggests that the key processing areas in these tasks are in the ventral stream, rather than it being the case that processing is ventral for the colour stimuli and dorsal for the luminance stimuli. The question remains as to how to account for the colour-luminance separation with the ventral stream hypothesis. Such outstanding issues may be resolvable with further experimentation on the transference of learning, for example, to find out if transference is possible between luminance and coloured stimuli in the modified task, and if transference takes place between stimuli of opposed cardinal colour direction.

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