Attention-based perceptual learning increases binocular rivalry suppression of irrelevant visual features

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Perceptual learning refers to an improvement on a perceptual task after repeated exposure to a stimulus. It has been shown that attention can play an important role in perceptual learning. Recently, it has been suggested that training can lead to increased suppression of information that is continuously irrelevant, and that this attention-based suppression plays an important role in more efficient noise exclusion. Here we investigate this claim. Observers performed a visual speed-discrimination task for 5 consecutive days. After training, sensitivity to motion directions that were relevant, irrelevant, or neutral toward the training task was assessed by measuring motion coherence thresholds. In addition, perceptual dominance during binocular rivalry was assessed for combinations of the three motion directions. The results showed that sensitivity to the task-relevant feature increased due to training. That is, motion coherence thresholds were selectively lowered for the task-relevant feature. Interestingly, the feature that was task-irrelevant during training was more strongly suppressed during binocular rivalry: The mean perceptual dominance of this feature was selectively decreased. Our results show that task-irrelevant information that potentially interferes with the primary task during learning gets more strongly suppressed. Furthermore, our results add new evidence in support of the claim that mechanisms involved in visual attention and binocular rivalry overlap.

Introduction

Perceptual learning refers to an improvement in performance on a perceptual task after repeated practice or exposure to a certain stimulus (Fahle & Poggio, 2002). Among its characteristics are a high specificity for spatial location (Crist, Kapadia, Westheimer, & Gilbert, 1997; Shiu & Pashler, 1992) and even for the exposed eye (Karni & Sagi, 1991). Another important characteristic is the high specificity for the trained feature: Feature-specific learning effects have been reported for attributes such as orientation (Fiorentini & Berardi, 1980; Ramachandran & Braddick, 1973), spatial frequency (Fiorentini & Berardi, 1980), and motion direction (Ball & Sekuler, 1982, 1987).

It has been shown that learning is more effective when the task-relevant visual signal is embedded in noise (Dosher & Lu, 1998, 1999; Gold, Bennett, & Sekuler, 1999; Li, Levi, & Klein, 2004), which might suggest that learning leads to an increased ability to exclude the task-irrelevant part of the visual input. What is noise and what is signal in a stimulus is, however, related to what part of the stimulus is relevant and what part is irrelevant to performing a behavioral task. Visual information that is relevant when performing task A might be completely irrelevant when performing task B. Thus, the specific task demands determine what part in a stimulus is relevant and will be selected, and what part is irrelevant and will be suppressed. In accordance to this, several studies have provided evidence that attention plays an important role in perceptual learning (for recent reviews, see Seitz & Dinse, 2007, and Seitz & Watanabe, 2005). Ahissar and Hochstein (1993), for example, conducted experiments in which observers performed different tasks on the same set of stimuli. Perceptual learning was limited to the task performed during training: When trained on task A and tested on task A, learning occurred; when trained on task A and tested on task B, learning did not transfer. Based on these results, the authors suggested that high-level attentional mechanisms are essential in perceptual learning. Furthermore, the results of a recent study (Vidnyánszky & Sohn, 2005) suggest that learning leads to more efficient

attentional suppression of the visual information that was task irrelevant during practice. Based on these results Vidnyánszky and Sohn (2005) suggested that increased inhibition of task-irrelevant information might be one of the underlying mechanisms of learning-induced improved noise exclusion.

Interestingly, even though there is strong evidence that attention can play an important role in perceptual learning, it has been shown that perceptual learning can also take place in the absence of attention (Watanabe et al., 2002; Watanabe, Náñez, & Sasaki, 2001). Watanabe et al. (2001) had observers perform a letter identification task on letters that were presented together with task-irrelevant background motion in a particular direction. The strength of this motion direction was set to a level ensuring it to be invisible to the observers, making this motion direction both irrelevant and imperceptible. After training, sensitivity to the motion direction that was present during training was increased selectively. Since the observers had not been aware of the motion in the background, this study shows that perceptual learning can also occur for information that is not attended during training.

The role of attention in perceptual learning has also been studied using electrophysiological recordings in behaving animals (Li et al., 2004; Op de Beeck, Wagemans, & Vogels, 2007; Polley, Steinberg, & Merzenich, 2006). For example, Polley et al. (2006) trained rats to attend to independent parameters: either frequency or intensity of an identical set of auditory stimuli. The results showed that the presence of irrelevant information (e.g., frequency information while attending to intensity) did not lead to learning of the irrelevant information. At first sight, these electrophysiological results—together with the earlier behavioral finding of Ahissar and Hochstein (1993)—appear to be at odds with the results of Watanabe et al. (2001). However, Polley et al. (2006) give a possible explanation for the discrepancy: In Watanabe's case the task-irrelevant information was presented at a sub-threshold level, whereas in their own case, the task-irrelevant information was at a supra-threshold level. They propose that "plasticity is restricted to the task-relevant domain only if stimuli in the task-irrelevant domain interfere with the ability to solve the task" (Polley et al., 2006, p. 4981). Support for this proposition comes from a recent study by Tsushima, Sasaki, and Watanabe (2006). In this study, observers performed a RSVP task in the presence of motion with variable strength. Performance on the RSVP task was maximally impaired when the strength of the motion was at a sub-threshold level. Interestingly, the lateral prefrontal cortex (LPFC), presumably involved in exerting inhibitory control of irrelevant signals (Dias, Robbins, & Roberts, 1996; Kerns et al., 2004; Knight, Staines, Swick, & Chao, 1999) became active when the motion strength was above perceptual threshold. The authors suggest that LPFC is involved in suppressing task-irrelevant signals: With supra-threshold motion, area LPFC inhibits the irrelevant motion; with sub-threshold

motion, however, LPFC remains inactive, leaving the irrelevant signals uninhibited.

In the present study, we investigate how learning-induced changes in the processing of visual features that were task relevant and task irrelevant during training will affect perceptual dominance of these features in binocular rivalry. In particular, we hypothesized that probing learning effects using binocular rivalry can provide evidence of increased suppression of task-irrelevant information due to training. During binocular rivalry, dissimilar images presented dichoptically compete for perceptual dominance (Alais & Blake, 2005; Blake & Logothetis, 2002). That is, each image undergoes alternating periods of perceptual dominance and suppression. It has been put forward that perceptual dominance durations (i.e., the mean duration each of the two is perceived) of the rival stimuli are affected by the perceptual strength of the stimuli (Levelt, 1965): A stronger stimulus will have a longer dominance duration than its rival (e.g., when its contrast is higher than its rival; Roelofs & Zeeman, 1919). Importantly, binocular rivalry is believed to involve suppressive interactions between neural pools processing the conflicting images (e.g., Blake, 1989; Tong & Engel, 2001; Wilson, 2003). Based on these premises, we hypothesize that if learning leads to increased inhibition of the visual feature that was task irrelevant during training, the dominance duration of this feature should decrease after compared to before training. To test this hypothesis, observers performed a speed-discrimination task on 5 consecutive days. The task was performed on rightward motion in the presence of task-irrelevant downward motion. In addition to the binocular rivalry experiment, motion coherence thresholds were acquired to assess learning-induced changes in sensitivity to the motion directions presented during training.

Method

Observers

Six naïve observers participated in the experiments. All observers had normal or corrected-to-normal vision.

Apparatus and stimuli

The stimuli used in the different experiments are schematically illustrated in Figure 1. The stimuli were presented using a Apple G4 dual 1000 MHz computer, on a 22′ LaCie III and a 22′ LaCie IV monitor (for the coherence and speed-discrimination experiment and for the rivalry experiment, respectively), at a refresh rate of 85 Hz. In the binocular rivalry experiment, a mirror-stereoscope was used to achieve dichoptic presentation of
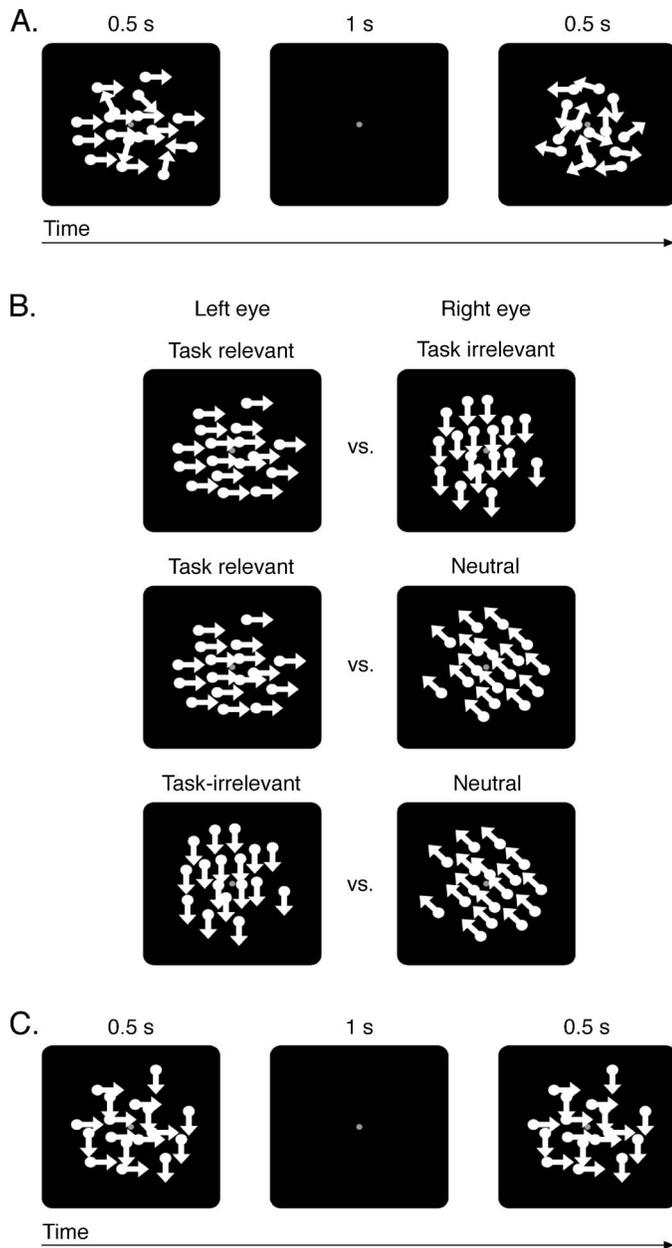
Figure 1. Schematic illustration of stimuli and conditions. A. The coherence threshold experiment. Before and after training, observers had to indicate which of two intervals contained global motion. By varying the percentage of dots moving in a single direction, 79% correct thresholds for rightward, downward, and left-upward were acquired. Thresholds were acquired using a staircase procedure (see text). B. The binocular rivalry experiment. Before and after training, observers continuously indicated which of two rivaling motion directions was perceptually dominant. Rival stimuli were rightward versus downward (relevant versus irrelevant; upper panel), rightward versus left-upward (relevant versus neutral; middle panel), and downward versus left-upward (irrelevant versus neutral; lower panel). C. The training experiment. On 5 consecutive days, observers indicated which of two intervals contained faster rightward motion. The speed of the vertical motion dots was constant; the speed of rightward motion was constant in one interval, and varied in the other.

the stimuli. In all experiments, circular apertures containing limited lifetime random dots were used. Stimuli were 1.1 deg in radius with a density of approximately 26 dots/deg^2. Individual dots were 0.1 deg in radius and moved at a speed of 3.2 deg/s (except during the training phase, where the speed of rightward motion was varied). Each dot appeared at a random position within the aperture, after which it made 40 steps along a single trajectory in a fixed direction. The coherence of the random dot stimuli was varied by changing the percentage of dots that moved in a certain direction. The luminance of the background and the dots was <1 cd/m^2 and 87.6 cd/m^2 for the LaCie III, and <1 and 61.1 cd/m^2 for the LaCie IV.

General procedure

Each observer performed in 3 experiments on 7 days. The maximum time allowed between sessions was 2 days. On day 1 and day 7, coherence thresholds were assessed for rightward (task-relevant), downward (task-irrelevant), and left-upward (task-neutral) motion. Also on day 1 and 7, perceptual dominance of combinations of these motion directions was assessed in the binocular rivalry experiment. On day 2 through 6, observers performed a speed-discrimination task for 30 min. For each experiment, observers viewed the stimuli at a distance of 57 cm from the monitor, with viewing distance restrained by a chinrest.

Motion coherence experiment

Motion coherence thresholds were acquired in separate blocks for each motion direction using a 3–1 adaptive staircase procedure arriving at a 79% correct threshold. A single trial consisted of 2 intervals, each 0.5 s in duration and separated by 1 s, one of which contained coherent motion in one of the 3 directions (rightward, downward, or left-upward), and one of which contained no coherent motion. The order of the two intervals was randomized from trial to trial. A single staircase terminated after 10 reversals. For each motion direction, 2 staircases (one starting at 0 and one starting 60% coherence) were randomly interleaved within one session. Thresholds were calculated by taking the mean of 9 staircases (where the mean of a single trail was based on the last 3 reversals in the staircase).

Binocular rivalry experiment

Perceptual dominance of the different motion directions was assessed by dichoptically presenting rightward versus downward, rightward versus left-upward, and downward versus left-upward motion. All random dot stimuli contained 100% coherent motion. The speed of individual dots was constant at 3.2 deg/s. A single trial lasted 30 s.

Observer	Day 1	Day 2	Day 3	Day 4	Day 5
1	3.46	3.79	4.06	3.55	3.67
2	3.36	3.42	3.05	3.16	2.69
3	4.21	4.69	5.62	5.02	5.05
4	5.34	4.19	4.65	4.40	3.92
5	4.35	2.95	3.02	3.01	4.41
6	2.48	3.28	3.11	2.60	1.20
all	3.72	3.65	3.75	3.54	3.74

Table 1. Results of the training task for each observer and the pooled data (rows). The values in the cells refer to the slope of the fitted psychometric (Weibull) curve.

Each combination between 2 motion directions was presented 20 times. The presentation of rivalry pairs was counterbalanced for the two eyes.

Training

On each training day, observers performed a 2-interval forced-choice speed-discrimination task. Each interval contained both downward and rightward motion. The speed of the downward motion was constant (at 3.2 deg/s) throughout the training sessions. The speed of the rightward motion was fixed for one of the two intervals (at 3.2 deg/s), while that of the other interval was varied between 1.6 and 4.8 deg/s (using the method of constant stimuli). The motion coherence of both motion directions was 100%. Observers were instructed to indicate which of the two intervals contained faster rightward motion. The experiment involved 25 trials per condition per training day.

Results

Performance in the speed-discrimination task during the 5-day practice sessions is displayed in Table 1 and

Figure 2. Increases in the slope of the psychometric curve would be indicative of improvements on the speed-discrimination task. No significant changes in the slopes of the psychometric curves were found between consecutive training days.

Training had a significant effect on the sensitivity to the motion direction that was relevant during training. In Figure 3A, the change in motion coherence thresholds after training compared to before training is displayed. The motion coherence threshold for the task-relevant direction is significantly decreased after training, $T(5) = 2.15$, $p = .04$. The thresholds for the irrelevant-motion direction are unaffected by training, $T(5) = -.58$, $p = .3$, as are the thresholds for the neutral-motion direction, $T(5) = -.3$, $p = .78$.

Figures 3B and 3C display data for the binocular rivalry experiments performed before and after training. The figures represent the change in dominance after training compared to before training. From Figure 3B, it can be observed that the cumulative perceptual dominance of different motion directions was affected by training for the combinations between task-relevant and task-irrelevant motion and between task-irrelevant and neutral motion. This means that the percentage of time the task-irrelevant motion direction was perceived decreased as a result of training. The decrease in the percentage of time the task-irrelevant direction was perceived can, in principle, be caused by (1) a decrease in the average duration the task-irrelevant direction was perceived, (2) an increase in the time its rival was perceived, or (3) by a combination of (1) and (2). To find out what caused the change in perceptual dominance, we analyzed changes in mean dominance durations of the motion directions for each of the three combinations after training as compared to before training (Figure 3C). For the combination between task-relevant and task-irrelevant motion, the mean dominance of the task-relevant direction is unaltered, $T(5) = .36$, $p = .73$, whereas the dominance duration of the task-irrelevant direction is significantly decreased, $T(5) = -3.65$, $p < .01$. For the combination between task-relevant and the neutral direction, there is no change in dominance for both
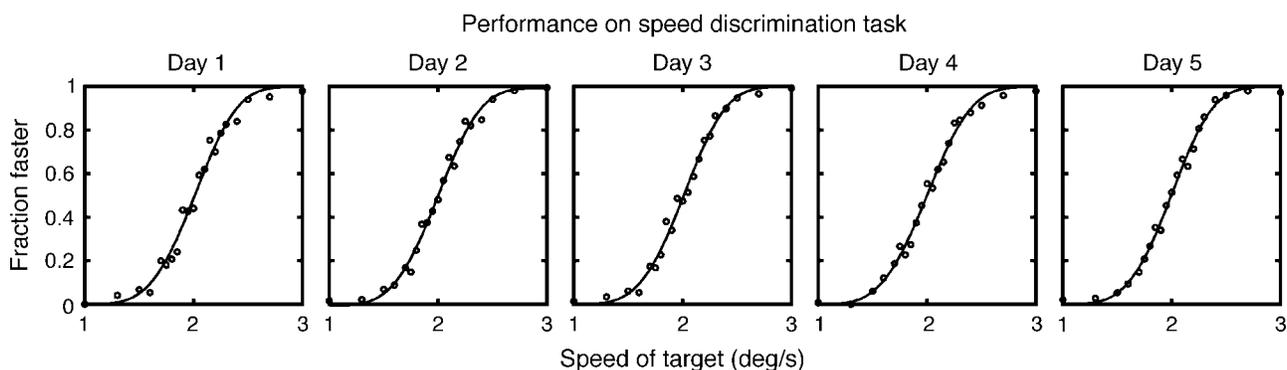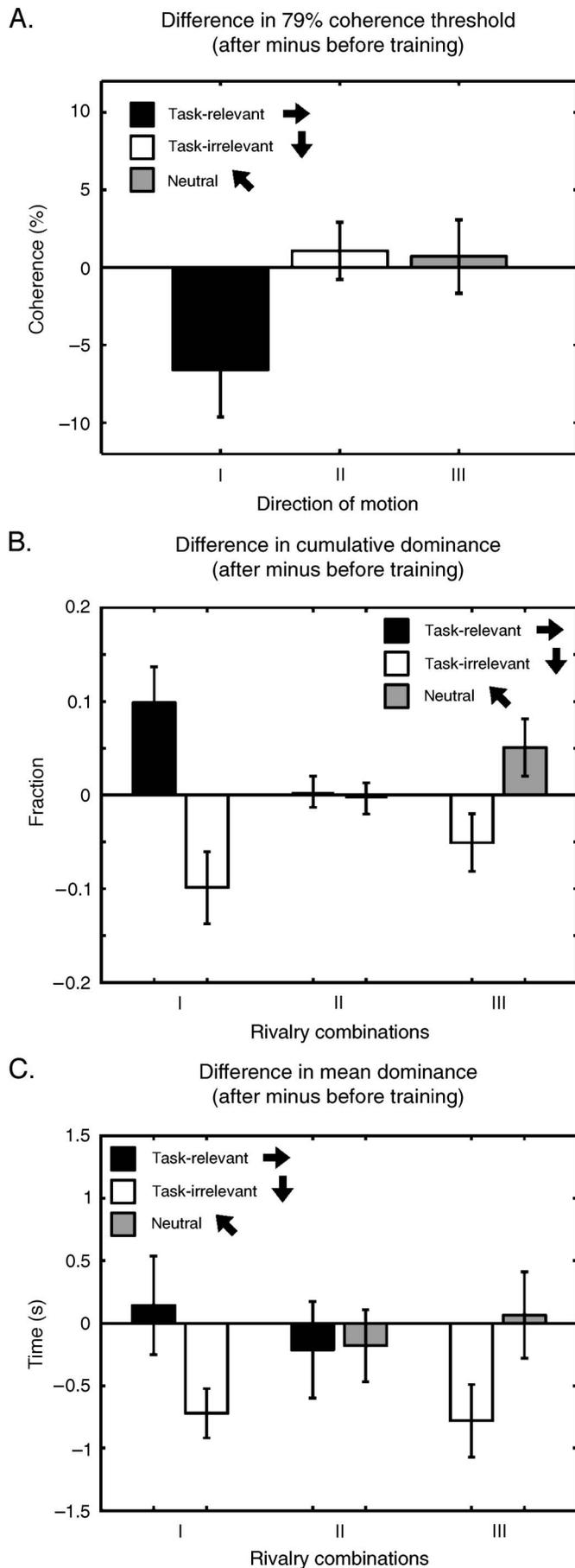
Figure 2. Pooled results for the 5-day training for 6 observers. Each panel represents the fraction "faster rightward motion" responses for each of the speeds of the rightward motion, for 5 consecutive days.

A.

Difference in 79% coherence threshold
(after minus before training)

Legend: Task-relevant ➡, Task-irrelevant ⬇, Neutral ◤

Y-axis: Coherence (%)
X-axis: Direction of motion (I, II, III)

B.

Difference in cumulative dominance
(after minus before training)

Legend: Task-relevant ➡, Task-irrelevant ⬇, Neutral ◤

Y-axis: Fraction
X-axis: Rivalry combinations (I, II, III)

C.

Difference in mean dominance
(after minus before training)

Legend: Task-relevant ➡, Task-irrelevant ⬇, Neutral ◤

Y-axis: Time (s)
X-axis: Rivalry combinations (I, II, III)

directions (task-relevant: $T(5) = -.55$, $p = .61$; neutral: $T(5) = -.62$, $p = .56$). For the combination between task irrelevant and neutral, the decrease in dominance for the task-irrelevant direction is significantly reduced, $T(5) = -2.68$, $p = .02$, whereas dominance for the neutral direction is unaltered, $T(5) = .19$, $p = .86$.

It has recently been argued that attention can influence the first percept during binocular rivalry (Chong & Blake, 2006; Mitchell, Stoner, & Reynolds, 2004). To find out whether our training had an effect on the initial percepts in our binocular rivalry experiments, we tested whether the fraction of first percepts for each of the three rivalry combinations was different before compared to after training. The results show that after training, the fraction of first *rightward* percepts is increased. Thus, for the combination between task relevant and task irrelevant, training leads to an increase in first task-relevant percepts, $T(5) = -3.23$, $p = .01$, as was the case for the combination between task relevant and neutral, $T(5) = -2.45$, $p = .03$. For the combination between task irrelevant and neutral, no difference in initial percepts was observed, $T(5) = .78$, $p = .47$. Important to note is that the overall change in perceptual dominance was not caused by the duration of the first percept. With this episode removed, the mean duration of the task-irrelevant motion was selectively decreased after training, $T(5) = -4.11$, $p < .01$ with task relevant, and $T(5) = -3.11$, $p = .01$ with neutral, while the dominance duration of other motion directions was unaffected.

Discussion

The main finding of the present study is that visual features that were task irrelevant throughout the training sessions were more strongly suppressed during binocular rivalry in the post-training compared to pre-training tests. These results show that learning results in stronger inhibition of irrelevant visual information that is present during training. In this respect, our findings are in agreement with a study by Vidnyánszky and Sohn (2005), who showed that the strength of the motion aftereffect (MAE) for a task-irrelevant motion direction

Figure 3. Training-induced changes in motion coherence thresholds and perceptual dominance during binocular rivalry. A. Results for the motion coherence experiments. The effect of training on motion coherence thresholds for rightward (task relevant), downward (task irrelevant), and left-upward (neutral) is expressed as the difference between thresholds before and after training. A negative value indicates a lowered threshold. The effect of training on perceptual dominance is expressed by the difference between cumulative (B) and mean dominance (C) durations before and after training. A negative value indicates decreased dominance.

was selectively decreased after compared to before learning. In their study it was also reported that the negative effect of learning (the decreased strength of the MAE) lasted up to 6 weeks after training. The latter finding suggests that the increased suppression of task-irrelevant features reported here will persist for—at least—several weeks. Taken together, the findings of Vidnyánszky and Sohn (2005) and the results reported here provide support for the suggestion that more efficient inhibition of task-irrelevant information might be one of the underlying mechanisms of learning-induced improved noise exclusion (Vidnyánszky & Sohn, 2005).

An important implication of our findings is that both facilitatory and inhibitory mechanisms of attentional selection are involved in perceptual learning, and that they can result in an enhancement and decrease of sensitivity to and perceptual strength of the visual information that is present during learning. It is the task relevance of the specific visual information during training that will determine whether learning will result in attention-based facilitation or suppression of its processing. Note that the existence of learning-induced attention-based inhibition has an important consequence with respect to the interpretation of the results of previous studies showing no learning effects in the case of unattended visual features (Ahissar & Hochstein, 1993; Polley et al., 2006; Shiu & Pashler, 1992). Instead of interpreting these results as evidence that attention is necessary for learning to take place, one might suggest that the lack of learning effects in these studies might be due to attention-based increased suppression of the visual information that was task irrelevant during training.

A puzzling aspect of our results is that learning-induced changes in direction sensitivity and binocular rivalry took place while improvement on the speed-discrimination task was absent. A possible reason for this might be that it has been reported that processing of speed and direction of visual motion can be independent (Matthews, Luber, Qian, & Lisanby, 2001; Matthews & Qian, 1999). Moreover, a study by Saffell and Matthews (2003) shows that learning curves are steeper for motion direction learning than for motion speed learning, which suggests that improvements in motion speed learning are generally modest. In that study it was also shown that speed learning did not transfer to direction discrimination, which—at first sight—seems to contradict our results. An important difference between our study and that of Saffell and Matthews (2003), however, is that our training stimulus contained two different motion directions, whereas the stimulus of Saffell and Matthews (2003) contained only one direction. Thus, although our training task involved speed discrimination, this task was performed on a single motion direction in the presence of another —irrelevant—motion direction. It remains an open question, however, why improvements in our speed-discrimination training were absent, while the training did selectively modulate both sensitivity to motion

direction and predominance of motion directions during binocular rivalry.

The increase in sensitivity for the task-relevant feature is in accordance with recent findings using a similar learning procedure (Tseng, Papathomas, & Vidnyánszky, 2006) and is also in line with the basic characteristics of perceptual learning: improved performance on a perceptual task, specific to the trained feature (e.g., Ball & Sekuler, 1982, 1987). No change in sensitivity was observed for a feature that was present, but task irrelevant. The same holds for a feature that was not presented during training. The latter implies that the increased sensitivity for the trained feature was not the result of learning of aspects of visual motion in general, or to a general improvement in performance on the motion coherence task. These results also show that our training task was sufficiently difficult, especially with respect to the finding that perceptual learning can generalize across motion directions if task difficulty is moderately difficult as opposed to when the task is difficult (Liu, 1999).

Another implication of the present study is that the effect of training is highly specific to the task used: in the binocular rivalry experiment, task-irrelevant information became less dominant (reflecting increased suppression of this feature), while dominance of task-relevant information was unaffected; in the coherence experiment on the other hand, sensitivity to task-relevant information was increased, while sensitivity to task-irrelevant information was unaffected. What can explain the different effects of training on motion coherence thresholds on the one hand, and on perceptual dominance during binocular rivalry on the other? To gain insight into this issue, it is informative to look at the visual processing stages that are thought to be involved in motion coherence tasks and in binocular rivalry. Global motion is generally believed to be computed at the level of the human homologue of monkey middle temporal (MT) and medial superior temporal (MST) area (Newsome & Paré, 1988). However, the computation of global motion presumably follows local motion processing in V1 (Albright & Stoner, 1995). Judging whether a stimulus contains global motion or not—as in our threshold experiment—therefore most likely will involve visual processing at the level of area MT. The decrease in motion coherence threshold for the task-relevant motion direction might therefore reflect increased sensitivity of MT cells for this motion direction. In line with this reasoning, it has been argued that MT plays a crucial role in perceptual learning of motion discrimination (Ball & Sekuler, 1982, 1987; Thompson & Liu, 2006; Vaina, Sundareswaran, & Harris, 1995; Zohary, Celebrini, Britten, & Newsome, 1994). Recently, area lateral intraparietal (LIP) has also been implicated in motion discrimination learning. For example, Freedman and Assad (2006) found that learning to categorize motion directions involved plasticity in LIP. This finding fits with the observation that area LIP plays an important role in decision making (e.g., Hanks, Ditterich, & Shadlen,

2006). However, classifying motion directions into relevant categories appears to be a more sophisticated task than performing a speed-discrimination task. Therefore, for our specific tasks, we suggest MT to be the most likely place for increased sensitivity to motion direction to task place.

As to the question on what processing stages are involved, the situation is more complicated for binocular rivalry, since there is a lively discussion in the literature on whether rivalry is instigated at early (Blake, 1989) or late (Logothetis, Leopold, & Sheinberg, 1996) stages of visual processing. Recently, however, it has been posed by several authors that a multitude of visual processing areas is involved in binocular rivalry (Blake & Logothetis, 2002; Nguyen, Freeman, & Alais, 2003; Wilson, 2003). Be that as it may, factors affecting the perceptual dominance of targets engaged in binocular rivalry point toward a crucial role of V1. For example, changing the contrast of the two rival targets—a manipulation that will strongly modulate V1 responses (Boynton, Engel, Glover, & Heeger, 1996)—will decrease the alternation rate of the rival targets (Roelofs & Zeeman, 1919). Therefore, the increased suppression of the task-irrelevant motion might reflect increased suppression of this stimulus at the level of V1. The hypothesis of stronger suppression in V1 is supported by a recent study by Nobre, Rao, and Chelazzi (2006), who found that suppression of task-irrelevant information was reflected by modulation of ERP components that reflect activity of early levels of perceptual analysis. It is, of course, possible that increased suppression at the level of V1 is caused by feedback from higher areas. In this respect, the results of Tsushima et al. (2006) provide a candidate neural mechanism. In their study, it was suggested that task-irrelevant information interfered with processing of task-relevant information because the task-irrelevant information remained unsuppressed by LPFC. If LPFC did suppress the task-irrelevant information, the authors argued, this information did not interfere with processing of the task-relevant information. These findings make it tempting to suggest that the modulation of perceptual dominance observed here might be the result of LPFC sending inhibitory signals to V1, where, as a result, the suppression of task-irrelevant information is increased.

A question that remains is why the increased sensitivity to the task-relevant feature was not reflected by increased dominance for this feature. The answer to this question can possibly lie in the fact that sensitivity to a certain visual feature does not necessarily correspond to the magnitude of perceptual dominance during binocular rivalry. For example, Fahle (1982) showed that a spatial frequency to which observers are usually most sensitive (which is around 3 cpd) does not make the most dominant stimulus during binocular rivalry. Also, oblique orientations (to which sensitivity is lower compared to horizontal and vertical orientations) do not have a lower perceptual dominance compared to horizontal or vertical orientations

(Fahle, 1982; Wade, 1974). Thus, although sensitivity was increased for task-relevant motion (as assessed by motion coherence thresholds), this increased sensitivity does not have to correspond to increased dominance of this feature during binocular rivalry. Likewise, the increased suppression of the task-irrelevant motion (as assessed by binocular rivalry) does not have to correspond to decreased sensitivity of this motion direction as indicated by an increased motion coherence threshold. Furthermore, the absence of increased dominance of the task-relevant feature due to training suggests that this feature did not become more salient due to training. Increased salience of stimuli has been linked to increased dominance during binocular rivalry in studies showing that recognizable figures and emotional stimuli predominate in rivalry (see Yu & Blake, 1992, and Alpers & Pauli, 2006, respectively) and that faces and recognizable words can overcome interocular suppression (Jiang, Costello, & He, 2007).

The results of the binocular rivalry experiments indicate that the stimulus feature that was irrelevant to the demands of the training task was more strongly suppressed when engaged in binocular rivalry. It is of interest to see our results in the framework of Levelt's second proposition (Levelt, 1965). As Levelt hypothesized, a decrease in strength of a rival stimulus will lead to an increase in mean dominance of its rival, leaving its own mean dominance unaffected (or put otherwise, decreasing a target's strength increases its suppression duration). Taking this proposition and applying it to our data would mean that the task-relevant stimulus became a stronger stimulus when presented with the task-irrelevant stimulus (Figure 3C, combination I), and that the neutral stimulus became stronger, also when presented with the task-irrelevant stimulus (Figure 3C, combination II). However, this would mean that both the task-relevant and neutral stimulus would have become stronger, which should have led to a decrease in their mean dominance durations when presented together. Although there is a slight decrease in their mean dominance, this is not significant. The fact that the dominance of the task-irrelevant motion is decreased in each of the rivalry combinations in which it was presented might suggest that suppression of this feature was increased in general. That is, the stimulus that was task irrelevant during training was more strongly suppressed during rivalry, irrespective of the precise nature of its rival.

The discrepancy between what would be expected from Levelt (1965) and our rivalry results can also be understood when taking a recent study by Brascamp, van Ee, Noest, Jacobs, and van den Berg (2006) into account. In their study, they showed that altering the contrast of a target—while keeping that of its rival constant—can in some situations lead to a change in its *own* mean dominance. This result is evidently in conflict with Levelt's second proposition, but is in line with our findings: A change in stimulus strength of a rival target

(the task-irrelevant one) was reflected by a decrease in its own dominance, and not by a change in dominance of its rival. In addition, in a study by Chong and Blake (2006), dominance durations were also selectively modulated by an attentional task: Dominance durations of the *attended* stimulus were selectively increased. The authors suggest that this inconsistency with respect to Levelt (1965) is due to the fact that attention can only be directed to a stimulus when it is visible, thereby limiting the effect that attention can have on binocular rivalry to the dominance durations of the attended stimulus. Their suggestion can be applied to our results: As suppression of an irrelevant stimulus increases when presented at a suprathreshold level during training (so it is consciously perceived during training; see "Introduction"), suppression of the irrelevant stimulus during binocular rivalry might be increased selectively while this stimulus is perceptually dominant, and not when it is perceptually suppressed. Put otherwise, our results suggest that increased suppression of an irrelevant visual feature due to training occurs when the feature is visible and not when it is invisible.

With respect to implications for binocular rivalry, our results are in agreement with the idea that mechanisms involved in selective attention and binocular rivalry overlap (Leopold & Logothetis, 1999; Stoner, Mitchell, Fallah, & Reynolds, 2005). During normal (binocular) vision, objects compete for representation or further processing (Desimone & Duncan, 1995). According to this biased-competition model of visual attention, competition is biased toward stimuli that are behaviorally relevant. Evidence is now accumulating that attention can have an immediate effect on binocular rivalry: Attention can bias the competition toward one of the rival targets (Chong, Tadin, & Blake, 2005; Lack, 1978; Meng & Tong, 2004; van Ee, van Dam, & Brouwer, 2005) as well as change its temporal dynamics (Paffen, Alais, & Verstraten, 2006). Recently, the effect of visual attention on the first percept during binocular rivalry was examined (Chong & Blake, 2006; Mitchell et al., 2004). The results of these studies show that the first percept during binocular rivalry can be biased toward the target that was previously attended. In our study we also find that the task demands biased the first percept during binocular rivalry. Interestingly, we find a different effect of training on initial percepts than on perceptual dominance: The initial percepts were biased toward the task-relevant feature, whereas perceptual dominance was selectively decreased for the task-irrelevant feature. This discrepancy might be explained by the fact that the effect of attention on initial dominance appears to be different its effect on subsequent dominance durations (Chong & Blake, 2006), a conclusion that also follows from a comparison between onset rivalry and subsequent perceptual dominance durations without attentional modulation (Carter & Cavanagh, 2007).

Conclusions

The present study shows that attentional suppression of task-irrelevant information increases with training. In addition, our results show that this training-induced suppression of task-irrelevant information can be accompanied by increased sensitivity for task-relevant information. We suggest that this attention-based suppression occurs when task-irrelevant information is strong enough to interfere with processing of the behaviorally relevant information in the stimulus.

Next to the implications on perceptual learning, our study provides new evidence regarding the proposed link between visual attention and binocular rivalry (Leopold & Logothetis, 1999; Stoner et al., 2005). While previous studies have shown that attention has an immediate modulatory effect on both predominance and initial dominance during binocular rivalry, our finding shows that attention also has a long-term influence on these two aspects of binocular rivalry. Specifically, our data suggest that the amount of attentional suppression (ignoring task-irrelevant information) covaries with the amount of binocular rivalry suppression.

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