

Effect of selective and distributed training on visual identification of orientation

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Abstract An experiment contrasted the effect of four training schedules in a visual orientation reproduction task. Two selective schedules involved repeated presentation of a single target orientation. Two non-selective schedules involved targets covering the first quadrant either at fixed, equispaced orientations, or distributed randomly. In pre-training sessions, we observed the classical oblique effect (precision for vertical and horizontal stimuli higher than for oblique ones). Practice improved precision with both distributed schedules, but was ineffectual for non-selective schedules. However, a significant oblique effect persisted under all conditions. We argue that the pattern of results is compatible with the hypothesis that the oblique effect reflects both the intrinsic neuronal properties of the primary visual system, and the structure of the visual space imposed by higher, more cognitive processes. The results challenge the thesis that only attentional and post-perceptual factors are able to affect the working of the early visual system.

Keywords Perceptual learning · Orientation · Training schedule · Vision

Introduction

An ongoing debate in visual science concerns the extent to which the early visual system is penetrable by non-visual inputs. The gamut of opinions encompasses some fairly drastic points of view. Recently, Pylyshyn (1999, 2003) has argued that the visual system includes a core component that is totally impervious to any kind of top-down influence, and that cognitive penetration occurs only in either pre- or post-perceptual stages. By contrast, the very notion of an inflexible core system driven exclusively by retinal inputs is rejected by Kosslyn who argues instead “there is no such thing as immaculate perception” (Kosslyn and Sussman 1995). The discontinuity thesis between perception and cognition defended by Pylyshyn has the merit of being testable. Perceptual learning affords one possible test.

According to Pylyshyn (2003), the fact that experience alters the way people discriminate stimulus properties can be credited to their increased ability to allocate proficiently the available attentional resources, not to changes in the working of the visual system, which remains impenetrable to cognitive factors. The role of attention in visual tasks is well established. The involvement of cognitive factors has been demonstrated in many double-task conditions where the allocation of attentional resources to a primary task induces a “cognitive tunnel vision” (e.g. Ikeda and Takeuchi 1975; Tschopp et al. 1999). Moreover, uncertainty about the discriminating features (Vogels et al. 1988) and interference between two discrimination tasks separated in visual space (Duncan 1984) induce a dramatic drop in performance. However, if one were able to show that perceptual learning also occurs in a discrimination task where the observer has no way of developing a strategy for focussing visual attention to improve performance, Pylyshyn’s impenetrability thesis would be challenged. One such task

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is to identify and to memorize the orientation of line stimuli varying randomly from trial to trial. Indeed, the fact that orientation ranges unpredictably over a wide interval prevents the observer from allocating attention in a systematic way to a restricted portion of the visual space.

The visual perception of line orientation is anisotropic. Vertical and horizontal directions are perceived with greater precision than oblique directions (the so-called “oblique effect”). The origin of the effect is still debated (Gentaz et al. 2008; Meng and Qian 2005; Westheimer 2003). Two sets of results on perceptual learning of orientation suggest the involvement of hardwired properties of the visual system.

First, Vogels and Orban (1985) showed that the oblique effect persists even after intensive selective training. Observers in an identification task judged whether a stimulus was tilted clockwise or counterclockwise with respect to the reference line (vertical, horizontal, or oblique). Practice reduced thresholds for all orientations, the improvement being stronger for oblique orientations than for vertical and horizontal ones. However, albeit reduced, the oblique effect persisted even after 5000 trials.

Second, learning does not transfer either to other orientations or to other localizations in the visual field. Both Vogels and Orban (1985) and two later studies (Schoups et al. 1995; Shiu and Pashler 1992) showed that thresholds for practiced orientations decrease more than thresholds for unpracticed ones. Moreover, Shiu and Pashler (1992) presenting oblique lines at 7 and 9.8 deg from the vertical at various eccentricities in the visual field (from 5 to 8 deg), demonstrated that the improvement in orientation discrimination after a 528-trial training does not transfer either to the opposite visual hemifield or to the opposite quadrant within the same hemifield. This was confirmed also by Schoups et al. (1995) by comparing a circular one-dimensional grating with light and dark bars spaced irregularly around a unique 45 deg oblique reference.

At the same time, there is converging evidence that the oblique effect also depends on cognitive processes. Because the orientation discrimination task is necessarily successive, memory is likely to play an important role. Moreover, Shiu and Pashler (1992) showed that practice does not improve orientation discrimination when observers were asked to attend to the brightness rather than the orientation of the stimuli, implying that perceptual learning can be gated by attention. The study already quoted by Schoups et al. (1995) reported an almost complete transfer of learning between eyes, which suggests the involvement of processes beyond those active in the early visual system. Other authors (Heeley and Buchanan-Smith 1992; Matthews et al. 1999, 2005; Westheimer 2003) have also argued along the same lines. Finally, there is evidence that additional factors

independent of the visual stimulus are also at work, suggesting that the processes responsible for the visual oblique effect are distributed and non-modality specific (Gentaz et al. 2008; Heeley et al. 1997; Luyat and Gentaz 2002).

The aim of our experiment was to investigate the effect of training on the perception of spatial orientations using training paradigms that prevent the focussing of attention on a limited portion of the visual field. If non-selective practice resulted in a significant amount of modality-specific plasticity even under such conditions, it could be argued that even such a basic function of the visual system as orientation identification is not as impenetrable as suggested by Pylyshyn (1999, 2003). We contrasted two types of training paradigms. One involved intensive training at fixed orientations. The other adopted a global training schedule, involving several reference orientations in the first quadrant, either fixed, or distributed randomly.

Method

Participants

Twenty-seven students of the University of Geneva participated in the experiment (14 females, 13 males; age range: 20–30 years; $m = 24.90$; $sd = 3.41$). All participants had normal or corrected-to-normal vision with no clinically reported astigmatism. The experimental protocol was approved by the Ethical Committee of the University of Geneva.

Experimental setup and stimuli

The experiment took place in a dark room. Stimuli were generated at a resolution of 1600×1200 pixels and presented on an Elo 2125c computer screen with a refresh rate of 85 Hz. Participants were seated at a viewing distance of 57 cm from the screen. To suppress external references, the screen was covered by a conical panel with a round opening for fitting the face. Head movements were minimized by a forehead-and-chin support. The height of the support was adjusted individually to keep the participants' eyes level with the center of the screen.

Stimuli were green bars (length: 15 deg; width: 0.184 deg) presented against a black background (preliminary tests showed that participant perceived the color green as more comfortable than white). To suppress aliasing artifacts, the edges of the bar were smoothed by a 2-pixel window set to intermediate colors and luminance. This window effectively eliminated sampling discontinuities at all orientations. We used bars instead of fuzzy stimuli (such as Gabor's patches) because this study is part of a larger project in which we also tested learning effects in the haptic

modality (blindfolded participants explored manually a rod with varying orientations). In order to be able to make meaningful comparisons between perceptual modalities, it was necessary to keep all other experimental parameters as similar as possible. Visual persistence after the presentation of the reference stimulus was suppressed by a visual blur of 200 3-pixel-wide dots randomly distributed over the screen and flickering at 25 cps.

Procedure

Testing was binocular. The experiment included three phases. The first phase (*pre-training*) estimated naïve performance for each participant. Trials began with a 2 s blur with flickering dots. Immediately after, a reference bar appeared for 2 s in the center of the screen with an orientation chosen randomly among 10 fixed values (0, 3, 15, 30, 45, 60, 75, 87, 90, and 135 deg). In this and the subsequent phases, during the 2 s reference presentation, participants were asked to fixate the center of the bar and avoid exploratory eye movements. However, eye position was not monitored. Following a second 2-s blur, a response bar appeared whose orientation deviated from that of the reference (clockwise or counterclockwise) by a random angle distributed uniformly between 15 and 25 deg. The participants had to reproduce as accurately as possible the remembered orientation of the reference with the help of a keypad. The response bar could be rotated either in 0.05 deg steps by pressing the keys once, or slowly and smoothly by a continuous pressure. Final judgments were entered by pressing the Enter key. The pre-training session included 10 trials of each orientation, for a total of 100 trials.

The subsequent phase (*training*) was spread over six sessions, 3 days apart. Participants were divided into four groups, each tested with a different training schedule. For 12 participants, practice was restricted to one orientation, either at 0 deg (group S_0 , $N = 6$) or 45 deg (group S_{45} , $N = 6$). For the remaining 15 participants, orientations in the first quadrant (0–90 deg) were presented, either the same fixed ones tested in the pre-training phase (i.e. by excluding the 135 deg orientation; group D_F ; $N = 7$), or distributed uniformly at random (group D_R ; $N = 8$). Visual feedback on angular error was provided after each trial by presenting simultaneously the reference (in green) and the response bar (in red). Each training session included 90 trials (90 repetitions for groups S_0 and S_{45} ; $10[\text{repetitions}] \times 9[\text{orientations}]$ for group D_F ; 90 random orientations for group D_R). Group sizes were not equal because five participants were not able to complete all training sessions.

In the third and final phase (*post-training*), we evaluated again individual performances using the same orientations and the same paradigm of the pre-training phase. This was

done twice, 3 days after the last training session (*post-training 1*), and 1 week later (*post-training 2*).

Data analysis

Performance was characterized by precision (variable error) estimated by the standard deviation of the responses around their mean. First, we computed precision for each participant. Then, individual estimates were averaged for each tested orientation. Because standard deviations never exceeded 20 deg, we used linear rather than circular statistics. Whenever appropriate, the General Linear Model (GLM) for the analysis of variance was used to test precision differences among conditions. Partial Eta Square (PES) values are provided for significant effects.

Results

Precision in the pre-training phase was highly dependent on orientation, reflecting a large perceptual anisotropy (Fig. 1). As expected, before training, the four experimental groups of participants were not significantly different (Two-way ANOVA $4[\text{group}] \times 10[\text{orientation}]$; group: $F(3,230) = 0.513$, $P = 0.674$; orientation: $F(9,230) = 55.90$, PES = 0.686, $P < 0.001$).

Training was globally effective (GLM, repeated measures, $4[\text{group}] \times 6[\text{session}]$; session: $F(5,115) = 16.42$, PES = 0.401, $P < 0.0001$; group: $F(3,23) = 26.61$, PES = 0.945,

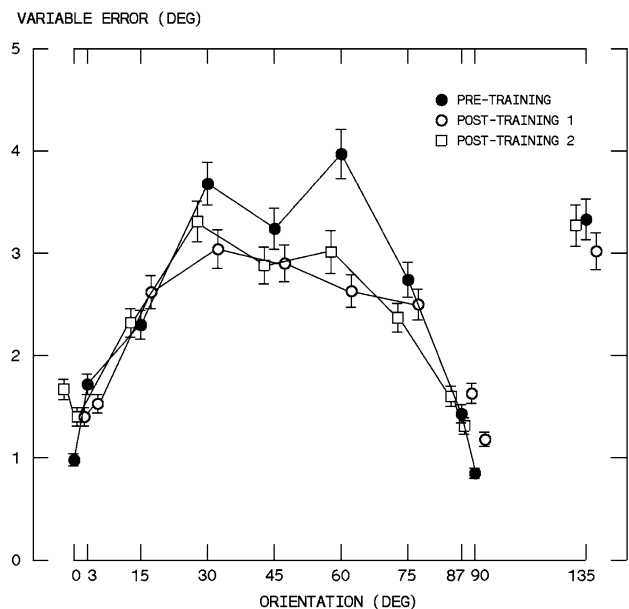


Fig. 1 Mean over all training schedules and all trials of reproduction precision (variable error) as a function of orientation for pre-training (filled circle) and post-training sessions (1: open circle; 2: open square). Bars indicate standard errors

$P < 0.0001$; group \times session: $F(15,115) = 3.35$, $PES = 0.280$, $P < 0.0001$).

As signaled by the significant interaction, different groups responded differently to training. Precision of group S_0 was uniformly very high (about 0.5 deg) and not significantly different between the first and the last session (Fig. 2). Precision of the other groups (S_{45} , D_F , and D_R) was much lower and improved with training. The improvement in D_F and D_R was not statistically different (GLM, repeated measures $2[\text{group}] \times 6[\text{session}]$, group: $F(1,13) = 0.025$, $P = 0.878$; session: $F(5,65) = 8.892$, $PES = 0.406$, $P < 0.0001$; group \times session: $F(5,65) = 1.341$, $P = 0.258$). Finally, learning leveled out faster for group S_{45} than for the groups following distributed schedules (pooling the results for groups D_R and D_F , two-way ANOVA $2[\text{group}] \times 6[\text{session}]$, group \times session: $F(5,95) = 3.144$, $PES = 0.142$, $P = 0.011$).

Performances in the two post-training phases (Fig. 1) were comparable (GLM, repeated measures, $10[\text{orientation}] \times 2[\text{post-training}]$, orientation: $F(9,260) = 23.105$; $PES = 0.444$,

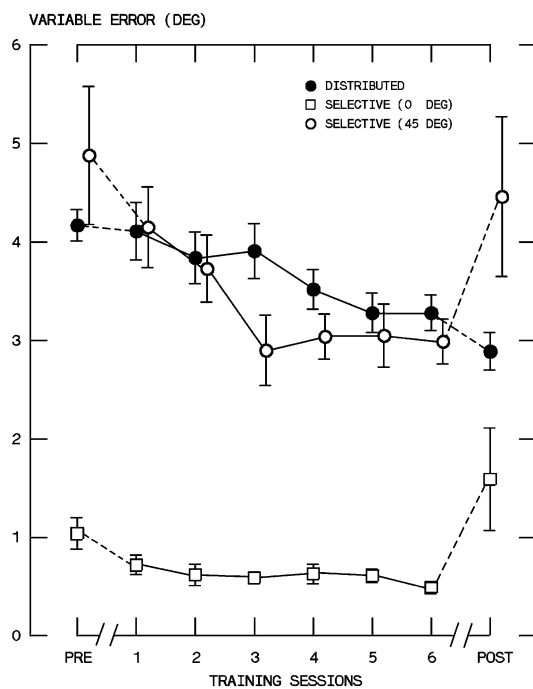


Fig. 2 Time course of precision across training sessions. Mean and standard error of the variable error over all trials. Different symbols identify the testing conditions. *Filled circle* pooled results for distributed schedules (groups D_F and D_R), which were not statistically different (see text); *open square* selective schedule (group S_0); *open circle* selective schedule (group S_{45}). For D_F and D_R , the results were collapsed over all tested orientations. For S_0 and S_{45} , the results are relative only to the orientation 0 and 45 deg, respectively. Precision for group S_0 was very high and virtually unaffected by training. Also reported the precision in the pre-training session and the post-training sessions (results only for trained orientations). Note that the data points for pre- and post-training are only relative to the orientations that were actually trained

$P < 0.0001$, post-training: $F(1,260) = 1.408$, $P = 0.237$), meaning that whatever change had been induced by training persisted for at least 1 week (see “Method”). Thus, the results for the two post-training phases were pooled.

A large difference among schedules emerged again by comparing performances before and after training (Fig. 2, PRE vs. POST). As for groups D_F and D_R following distributed schedules, the performance improvement gained through learning persisted for several days. Because the effect of training was similar (see above), statistical analysis was performed on the pooled results of the two groups ($N = 15$). The average precision over all orientations in the POST phase was significantly higher than in the PRE phase (paired t test, $t(14) = 2.681$, $P = 0.009$). Actually, precision was marginally better in the POST phase (2.89 deg) than in the last training session (3.28 deg). In contrast, in spite of the intensive 540-trial practice, whatever improvement resulted from selective schedules (groups S_0 and S_{45}) vanished in the post-training phase. We compared separately for the two groups, the precision at the trained orientations in the PRE and POST phases. For group S_{45} , mean precision was almost identical (PRE: 4.88 deg; POST: 4.46 deg, paired t test, $t(5) = 1.650$, $P = 0.133$). For group S_0 , precision was even slightly worse after training (PRE: 1.04 deg; POST: 1.59 deg, paired t test, $t(5) = -0.886$, $P = 0.398$).

Over and above the differences among groups, precision continued to depend on orientation even after training (Fig. 1). However, the contrast between groups D_F and D_R on the one side and groups S_0 and S_{45} on the other side extended to all orientations. When all orientations are taken into account, post-training performance of groups S_0 and S_{45} was statistically indistinguishable (Two-way ANOVA, $2[\text{group}] \times 10[\text{orientation}]$, group: $F(1,100) = 2.481$, $P = 0.118$; orientation: $F(9,100) = 14.830$, $PES = 0.572$, $P < 0.0001$; group \times orientation: $F(9,100) = 1.388$, $P = 0.204$). Figure 3 compares pre- and post-training performances for fixed schedules (results for groups S_0 and S_{45} were pooled for this comparison).

Globally, there was no difference between the oblique effect in pre- and post-training sessions (GLM, repeated measures, $2[\text{pre/post-training session}] \times 10[\text{orientation}]$; session: $F(1,110) = 1.279$, $P = 0.260$; orientation \times session: $F(9,110) = 1.662$, $P = 0.107$). Moreover, none of the pairwise differences for the same orientation was significant. In contrast, the same comparison for distributed schedules (Fig. 4, results for groups D_F and D_R were again pooled) demonstrates that a substantial amount of generalized learning persisted in the post-training phases (GLM, repeated measures, $2[\text{pre/post-training session}] \times 10[\text{orientation}]$ session: $F(1,140) = 63.929$, $PES = 0.344$, $P < 0.0001$; orientation \times session: $F(9,140) = 4.612$, $PES = 0.240$, $P < 0.0001$). Specifically, there were significant improvements at 3

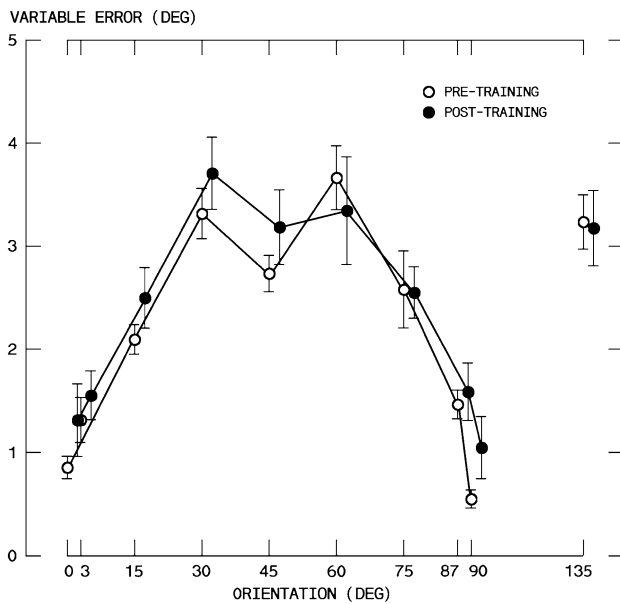


Fig. 3 Effect of fixed training schedules on variable error. Mean and standard error of the variable error over all trials and participants in groups S_0 and S_{45} as a function of stimulus orientation (*open circle* pre-training; *filled circle* post-training)

($t(14) = 4.953$, $P < 0.0001$), 30 ($t(14) = 3.220$; $P = 0.006$), 45 ($t(14) = 4.881$; $P < 0.0001$), and 60 deg ($t(14) = 4.501$; $P < 0.0001$). Finally, it should be stressed that, although the improvement in precision obtained with non-selective training schedules was mostly concentrated on the central orientations, it did however transfer also to the untrained 135 deg diagonal orientation. Indeed, precision for this orientation pooled over D_F and D_R was significantly better in the post-training (2.315 deg) than in the pre-training (3.131 deg) phase (paired t test, $t(14) = 2.340$, $P = 0.035$).

Discussion

A reproduction task investigated the conditions under which visual identification of spatial orientations can be affected by training. We contrasted the single-orientation schedule adopted in several previous studies (see “[Introduction](#)”) with two schedules in which training involved several orientations in the [0–90 deg] quadrant. In the latter case, the stimulus to be matched varied unpredictably from trial to trial, preventing the possibility for the participants to elaborate a principled strategy for focussing attention on a limited region of the visual space.

At the population level, the results confirmed that the visual oblique effect persists after training (Schoups et al. 1995; Shiu and Pashler 1992; Vogels and Orban 1985; Vogels et al. 1988). Globally, practice improved the precision of responses (Fig. 1). The improvement during the

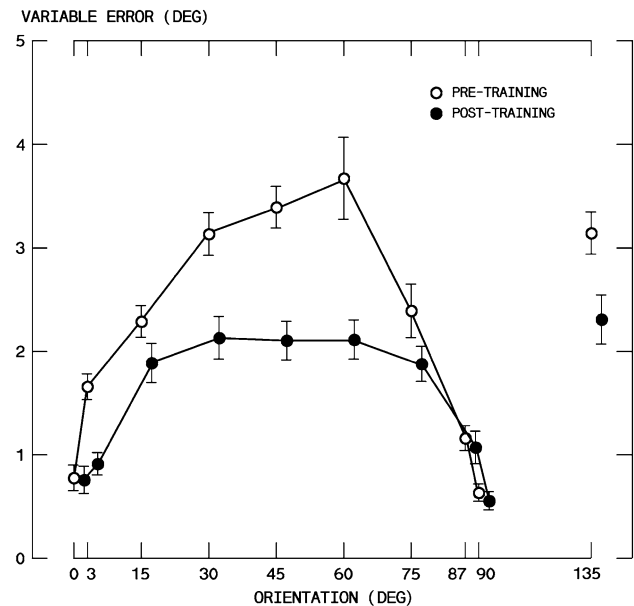


Fig. 4 Effect of global training schedules on precision. Mean and standard error of the variable error over all trials and participants in groups D_F and D_R as a function of stimulus orientation (*open circle* pre-training; *filled circle* post-training). Note that the improvement in precision generalized also to the 135 deg orientation that was trained

training sessions was only marginal for group S_0 because precision was always very high for this cardinal orientation. Instead, in the three other groups, precision improved by at least 25% at the end of training (Fig. 1). Yet, the oblique effect was not suppressed. This is indeed what would be predicted by the hypothesis that the oblique effect reflects at least in part the properties of the early visual system.

The most important result emerged when we contrasted the two types of training schedules. When participants were trained at fixed orientations (groups S_0 and S_{45}), whatever improvement in precision was brought about by training disappeared in the post-tests, either at the trained or at any other orientation. Instead in groups trained by stimuli spanning, the entire [0–90 deg] quadrant (D_F and D_R), the improvement persisted even 1 week after the first post-test. It should be stressed that the crucial factor was the nature of the training (selective vs. distributed) rather than the total number of trials. For instance, at the 45 deg orientation, the effect of 6[sessions] \times 90[repetitions] = 540 trials with the selective schedule (group S_{45}) was far smaller than the effect of the 6[sessions] \times 10[repetitions] = 60 trials with the same orientation with the non-selective schedule (group D_F). It should also be stressed that in both global training schedules the improvement of the precision observed in the first quadrant transferred completely to the diagonal in the second quadrant (135 deg), which was never trained.

As recalled in the “[Introduction](#)”, although hardwired properties of the visual system are likely to play a role in

the anisotropic perception of orientations, studies contrasting orientation discrimination with simultaneous and successive presentations (Heeley and Buchanan-Smith 1992; Matthews et al. 2005; Westheimer 2003) have already suggested the presence of other more cognitive factors. In particular, Heeley and Buchanan-Smith (1992) demonstrated that the oblique effect drops (but does not disappear) in the simultaneous condition, suggesting that perceptual anisotropy may originate within a visual memory storage mechanism. Furthermore, by using successive Gabor patches Matthews et al. (2005) have shown that the difference between the precision at cardinal and oblique orientations increases almost linearly with stimulus duration. Thus, even the contribution of the hardwired low-level visual mechanisms is dynamic in nature. Our results invite a similar conclusion. The very existence of a training transfer across orientations, the marked difference between the outcomes of selective and non-selective training schedules, and the fact that the improvement of the performance in groups D_F and D_R was mostly concentrated at the three central orientations 30, 45, and 60 deg all concur to suggest that the anisotropy results from the conjunction of two causes, only the one of which is pervious to training (see below). Arguably, this modifiable source of anisotropy is due to a cognitive bias in the encoding and memorization of orientation. Several hypotheses may be advanced concerning the nature of this bias.

One hypothesis is that orientations are recoded in categorical terms (Huttenlocher et al. 1991; Heeley and Buchanan-Smith 1992). The idea is that visual space is partitioned into quadrants delimited by the vertical and horizontal orientations, each quadrant corresponding to a different category. Responses would then result from the interaction between a low-level (supposedly veridical) representation of the stimulus orientation and a higher process that, by assigning the stimulus to one of the categories, associates it to the corresponding centre (i.e., one of the diagonals). The hypothesis may account for the distribution of systematic biases. However, it is not clear how the categorical hypothesis may account for the striking difference between selective and non-selective training schedules in their ability to improve precision.

An alternative hypothesis is that the visual system has a built-in frame of reference with vertical and horizontal axes. The hypothesis is supported by considerable evidence from the anatomy of the visual pathways and by the fact that at least the vertical direction is invariably defined by the gravitational force. If so, vertical and horizontal stimuli would be identified most accurately because the directional tuning of the early visual system is further enhanced by the availability of stable reference axes. Instead, oblique stimuli for which direct neuronal coding is already less accurate than that of cardinal stimuli might require a further computation,

such as that of the ratio of the two projections on the reference axes (Westheimer 2003). According to this view, the modifiable component of the oblique effect reflects the uncertainties associated with the additional processing needed to encode oblique orientations (Gentaz et al. 2008; Luyat and Gentaz 2002).

The second hypothesis accommodates better than the first one the relation between orientation and precision (Figs. 3, 4). We may distinguish two regions within the explored visual quadrant. Within the small (<3 deg) sectors that straddle each cardinal axes stimuli were discriminated with striking precision. In the second region extending between 3 and 75 deg, the oblique effect increases and then decreases again. It is also within this region that the effect of training was concentrated for the two groups trained with non-selective schedules (groups D_F and D_R). Recent experiments showing similar oblique effects in direction perception, smooth pursuit eye movements (Krukowski and Stone 2005) and manual pointing movements (Smyrnis et al. 2007) support the notion that the anisotropy is due to cortical signals that are directionally biased to emphasize the cardinal directions. The results of these experiments also fit nicely with the suggested distinction between the regions of the visual space centered on the cardinal directions and the regions around the oblique directions.

As anticipated above, the contrast between the two regions suggests that the oblique effect results from the combined action of two sources. On the one side, the ± 1.5 deg uncertainty affecting the estimation near the horizontal and vertical directions may correspond to the intrinsic limit of the combined action of neuronal mechanisms and the available stable axes of reference. These being hard-wired limits set by the properties of the early visual system, it is not surprising that they are not modified by any amount of practice. On the other hand, as suggested above, dealing with oblique stimuli is likely to involve additional processing involving a frame of reference. If so, the reliability with which the visual system carries out the computations to encode the orientation of the stimuli, and to match its memory trace to the response bar may depend on the stability of the reference frame. This line of reasoning suggests that distributed training schedules have a beneficial effect insofar as they affect mechanisms that are independent of the actual orientation of the stimuli. We recall that participants tested with distributed schedules (groups D_F and D_G) could not focus their attention on any specific region of the working quadrant because stimuli were presented at random orientations. Therefore, the beneficial effect of training cannot be accounted for by a progressive sharpening of the attentional window (such a sharpening may explain why precision in the early training sessions improved faster in group S_{45} than with either distributed schedules, see Fig. 2). We hold instead that, by forcing

them to reproduce the stimulus orientation across the entire quadrant, the feedback continuously provided during training did improve the stability of the perceptual frame of reference. Crediting the reduction of the oblique effect to the establishment of a more stable frame of reference may also explain why performance improved also for stimuli at 135 deg for which no feed-back was ever provided. Indeed, such an improvement is conceivable when feed-back is provided across the entire quadrant, but not when just one fixed stimulus is presented repeatedly.

Finally, we take up the implications of the results vis-à-vis the debate evoked in the introduction on the cognitive penetrability of the visual system. We recall that Pylyshyn's impenetrability thesis acknowledges only two possible ways for cognition to influence visual perception: (1) a selective allocation of attention, either extrinsically, by virtue of certain properties of the stimulus, or intrinsically, i.e. by an act of will; (2) the post-visual processing involved in identifying the stimulus as something familiar, or in manipulating it mentally. As for point (1) above, we stress again the key difference between selective (group S_0 and S_{45}) and distributed schedules (groups D_F and D_R). In the former case, observers were likely to focus attention on the unique orientation that was presented repeatedly. In contrast, when the orientation varied randomly from trial to trial (distributed schedules), a strategy for focussing attention in a principled way was no longer available. As for point (2), if the hypothesis that orientations are recoded in categorical terms were correct, such recoding may well be considered as an instance of post-visual processing. If so, our results would not challenge the impenetrability thesis because learning would not affect what Pylyshyn considers the impenetrable core module of vision. We argued, however, that the categorical hypothesis is inconsistent with the observed difference between selective and non-selective training schedules, and also inconsistent with the observed distribution of the variable errors. This leaves as a plausible alternative that the component of the oblique effect that is permeable to training reflects the stability of the reference frame within which oblique stimuli are represented. To the extent that the frame of reference can be considered as an integral ingredient of the early-vision machinery, this alternative would imply that—contrary to Pylyshyn hypothesis—at least one component of the early visual processing is not modular in a strict sense.

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References

- Duncan S (1984) Selective attention and the organization of visual system. *J Exp Psychol Gen* 114:501–517
- Gentaz E, Baud-Bovy G, Luyat M (2008) The haptic perception of spatial orientations. *Exp Brain Res* 187:331–348
- Heeley D, Buchanan-Smith H (1992) Orientation acuity estimated with simultaneous and successive procedures. *Spat Vis* 6:1–10
- Heeley D, Buchanan-Smith H, Cromwell J, Wright J (1997) The oblique effect in orientation acuity. *Vis Res* 32:235–242
- Huttenlocher J, Hedges LV, Duncan S (1991) Categories and particulars: prototypes effects in estimating spatial locations. *Psychol Rev* 98:352–376
- Ikeda M, Takeuchi T (1975) Influence of foveal load on the functional visual field. *Percept Psychophys* 18:255–260
- Kosslyn SM, Sussman AL (1995) Roles of imagery in perception: or, there is no such thing as immaculate perception. In: Gazzaniga MS (ed) *The cognitive neurosciences*. MIT Press, Cambridge, pp 1035–1042
- Krukowski AE, Stone LS (2005) Expansion of direction space around the cardinal axes revealed by smooth pursuit eye movements. *Neuron* 45:315–323
- Luyat M, Gentaz E (2002) Body tilt effect on the reproduction of orientations: studies on the visual oblique effect and subjective orientations. *J Exp Psychol Hum Percept Perform* 28:1002–1011
- Matthews N, Liu Z, Geesaman BJ, Qian N (1999) Perceptual learning on orientation and direction discrimination. *Vis Res* 39:3692–3701
- Matthews N, Rojewski A, Cox J (2005) Time course of the oblique effect in orientation judgments. *J Vis* 5:202–214
- Meng X, Qian N (2005) The oblique effect depends on perceived, rather than physical, orientation and direction. *Vis Res* 45:3402–3413
- Pylyshyn Z (1999) Is vision continuous with cognition? The case for cognitive impenetrability of visual perception. *Behav Brain Sci* 22:341–364
- Pylyshyn Z (2003) *Seeing and visualizing: it's not what you think*. MIT Press, Cambridge
- Schoups A, Vogels R, Orban G (1995) Human perceptual learning in identifying the oblique orientation: retinotopy, orientation specificity and monocularly. *J Physiol* 483:797–810
- Shiu L-P, Pashler H (1992) Improvement in line orientation discrimination is retinally local but dependent on cognitive set. *Percept Psychophys* 52:582–588
- Smyrnis N, Mantas A, Evdokimidis I (2007) “Motor oblique effects”: perceptual direction discrimination and pointing to memorized visual targets share the same preference for cardinal orientations. *J Neurophysiol* 97:1068–1077
- Tschopp C, Safran AB, Viviani P, Reicherts M, Bullinger A, Mermoud C, Rudaz N (1999) Does visual sensitivity improve between 5 and 8 years? A study of automated visual field examination. *Vis Res* 39:1107–1120
- Vogels R, Orban GA (1985) The effect of practice on the oblique effect in line orientation judgements. *Vis Res* 25:1679–1687
- Vogels R, Eeckhout H, Orban GA (1988) The effect of feature uncertainty on spatial discriminations. *Perception* 17:565–577
- Westheimer G (2003) Meridional anisotropy in visual processing: implications for the neural site of the oblique effect. *Vis Res* 43:2281–2289