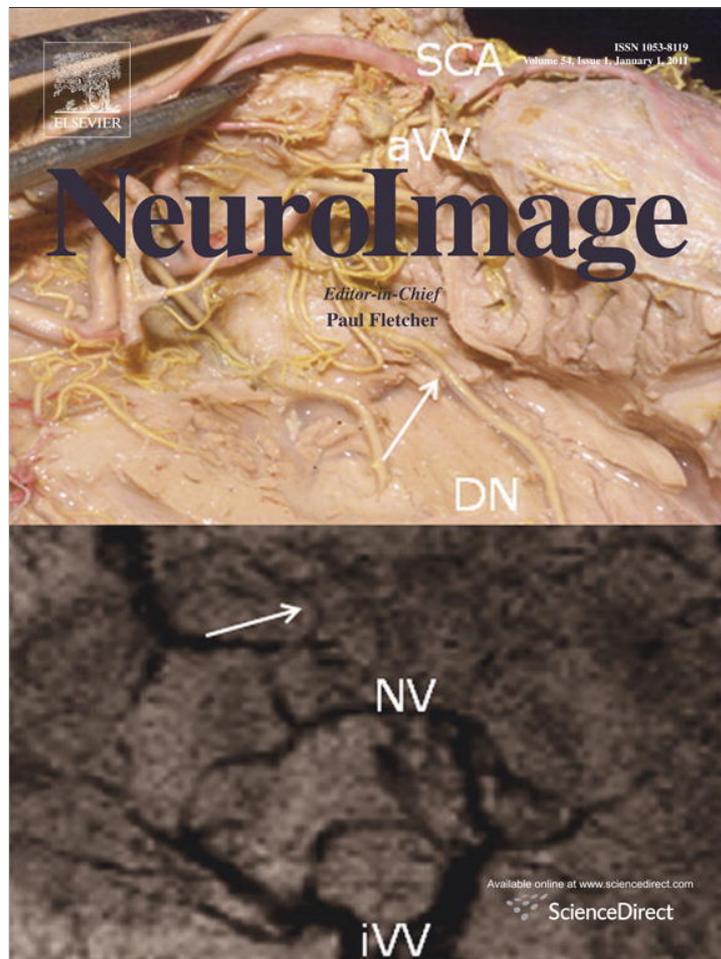


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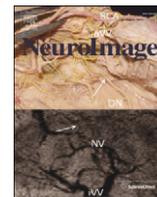
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Pattern motion representation in primary visual cortex is mediated by transcortical feedback

K.E. Schmidt^{a,*}, S.G. Lomber^b, B.R. Payne¹, R.A.W. Galuske^{a,c}

^a Independent Research Group, Cortical Function and Dynamics, Max-Planck Institute for Brain Research, Deutschordenstraße 46, 60528 Frankfurt/M, Germany

^b Centre for Brain and Mind, Department of Physiology and Pharmacology, Schulich School of Medicine and Dentistry, University of Western Ontario, London, Ontario, Canada N6A 5C1

^c Department of Biology, Technical University Darmstadt, Schnittspahnstr. 3, 64287 Darmstadt, Germany

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ABSTRACT

A highly important question in visual neuroscience is to identify where in the visual system information from different processing channels is integrated to form the complex scenery we perceive. A common view to this question is that information is processed hierarchically because small and selective receptive fields in lower visual areas melt into larger receptive fields in specialized higher visual areas. However, a higher order area in which all incoming signals ultimately converge has not yet been identified. Rather, modulation of subthreshold influences from outside the classical receptive field related to contextual integration occurs already in early visual areas. So far it is unclear how these influences are mediated (Gilbert, 1998; Angelucci and Bullier, 2003; Gilbert and Sigman, 2007). In the present study, we show that feedback connections from a higher motion processing area critically influence the integration of subthreshold global motion cues in early visual areas. Global motion cues are theoretically not discernible for a local motion detector in V1, however, imprints of pattern motion have been observed in this area (Guo et al., 2004; Schmidt et al., 2006). By combining reversible thermal deactivation and optical imaging of intrinsic signals we demonstrate that feedback signals from the posteromedial suprasylvian sulcus are critical for the discrimination between global and local motions already in early visual areas. These results suggest that global features of the visual scenery are fed back to lower visual processing units in order to facilitate the integration of local cues into a global construct.

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Introduction

In primary visual cortex, neurons have small receptive fields and are selective for contour orientation and linear motion. However, from the limited perspective of their receptive fields, the direction of motion is underspecified. In case of moving featureless lines, different motion vectors will be compatible with the motion seen through the circular aperture formed by their small local receptive field. Usually, motion “perceived” by the receptive field will be orthogonal to the line’s orientation, irrespective of the actual physical direction of global motion. Only neurons whose receptive fields cover also unambiguous motion cues such as end-points of lines can detect this global and “true” physical motion. Such neurons are only located in visual areas hierarchically higher than V1 and V2. Thus, it is commonly assumed that neurons in primary visual areas are not able to signal any global motion different from the motion orthogonal to the object’s

orientation. Accordingly, neurons in cat or macaque monkey V1 responding to parallel or global motion have rarely been found (Gizzi et al., 1990; Castelo-Branco et al., 2000; Geisler et al., 2001; Guo et al., 2004). However, on the population level subthreshold responses to the pattern and thus global direction of motion which differs from the local direction have been observed in cat area 18 (Schmidt et al., 2006). This is in agreement with the notion that neurons in early visual cortex receive modulatory influences from the context surrounding the classical receptive field (for review see Allman et al. (1985), Gilbert (1998) and Albright and Stoner (2002)). The emergence of such contextual influences has been attributed to both intrinsic and transcortical feedback connections from higher visual areas (Albright and Stoner, 2002; Angelucci and Bullier, 2003; Angelucci and Bressloff, 2006; Gilbert and Sigman, 2007). Global motion selective neurons have been found in higher motion processing areas like, for example, the monkey’s middle temporal area (MT) (Albright, 1984; Movshon et al., 1985), or the cat’s middle suprasylvian (MS) cortex (Li et al., 2001; Ouellette et al., 2004; Villeneuve et al., 2006). These areas are, therefore, in a good position to provide information about the global motion context and send it back to early visual areas. Cat MS cortex sends ample feedback connections to areas 17 and 18 (Symonds and Rosenquist, 1984;

* Corresponding author. NW2, Kortikale Funktion und Dynamik, Max-Planck-Institut für Hirnforschung, Deutschordenstraße 46, 60528 Frankfurt, Germany.

E-mail address: schmidt@mpih-frankfurt.mpg.de (K.E. Schmidt).

¹ Deceased and thus no affiliation.

Shipp and Grant, 1991; Payne and Lomber, 2003). Based on its connectivity the posteromedial part of this region (pMS) has been considered to be a homologue of monkey/human area MT (Payne, 1993) and, in accordance with this comparison, neurons are selective for the direction of movement and line orientation (Gizzi et al., 1990; Zumbroich and Blakemore, 1987; Danilov et al., 1995). Behaviourally, deactivation of MS cortex in cats resulted in deficits in visual orienting and in the detection of the direction of motion (Lomber et al., 1996). Previous imaging experiments have shown that feedback connections from MS cortex are crucial for the stability of direction maps and single cell responses evoked by moving lines or dots in area 18 (Galuske et al., 2002). In the cat, specialized neurons indicating the pattern direction of plaids have been observed in areas like the anterior ectosylvian cortex (AEV; Scannell et al., 1996) or the lateral posterior pulvinar (LP; Merabet et al., 1998). These areas can exert their influence on primary visual cortex mainly via the strong feedback connection of pMS cortex (Scannell et al., 1995; Payne and Lomber, 2003; Huppé-Gourgues et al., 2006). Therefore, pMS cortex may be in a key position for delivering global motion signals. To examine this possibility, we tested in how far feedback signals from MS cortex influence the pattern motion response to plaid stimuli in cat areas 17 and 18.

Methods

All animal experiments were performed in accordance with the guidelines for the use of animals in research of the Society for Neuroscience.

Optical imaging of intrinsic signals in areas 17 and 18 of six adult cats was combined with thermal deactivation of the posterior middle suprasylvian sulcus (pMS) (Lomber et al., 1999). Different data sets from four of these cats have been published as parts of two other studies (Galuske et al., 2002; Schmidt et al., 2006). One data set consisted of a cycle of optical recordings during baseline, cooling deactivation of ipsilateral pMS cortex, and recovery phase. In our study, 19 different data sets were obtained in six cats from different recording positions within areas 17 and 18 and different hemispheres. As within the same cat, pattern and component indices varied for different recording sites (see also Schmidt et al. (2006); their Fig. 2), we decided to treat them differently as separate measurements, i.e. up to three data sets per cat, one for area 17, one for central area 18 and one for a more anterior 18 position, respectively. Cats P, J, F and E contribute each with 3 data sets from one hemisphere, cat L with 2 data sets. Cat C had two probes implanted and contributes with both hemispheres and 5 data sets (two from area 17, two from central area 18 and one from a more anterior area 18 position).

PMS cryoloops and recording chambers were implanted 4–10 weeks prior to the principal experiment under inhalation anesthesia (N_2O (70%), O_2 (30%) and halothane (0.8%)). Four animals also had a second control loop placed, i.e. in primary auditory cortex, area 7, or posterior ectosylvian (PE) cortex (Galuske et al., 2002) and the effectiveness of the pMS cooling was behaviourally tested by visual field perimetry (Payne et al., 1996; Lomber and Payne, 2000). The completeness of pMS deactivation was confirmed because all cats neglected visual stimuli presented in the entire contracoiled, but not ipsicoiled, hemifield when the cryoloops were cooled down to 1–3 °C. As described earlier (Payne et al., 1996; Lomber and Payne, 1996), the deficit in the contralateral field would have been incomplete if the loops were not deactivating pMS in its entirety.

Visual stimulation

Area 17 and area 18 were discriminated by stimulating with gratings of different spatial frequency. In order to obtain baseline orientation preference maps we presented whole-field square-wave gratings of four orientations (0.1 c/deg for area 18 positions and 0.5 c/

deg for area 17 positions) drifting in the two orthogonal directions at 16 deg/s (area 18) or 4 deg/s (area 17). The test stimulus consisted of four different plaid stimuli (see Table 1 in Schmidt et al. (2006) for detailed luminance values), two extreme pattern and non-pattern biased (NPB 1 and PB 1) and two more intermediate constructs. Stimulus choice was guided by the publications of Stoner et al. (1990) and Castelo-Branco et al. (2000). Previously, we have shown that cats differentiate these two extreme cases (Schmidt et al., 2006). To construct the plaid stimuli, square-wave gratings were superimposed in a circular display subtending 24° of visual angle. The velocity of the pattern movement was $8^\circ s^{-1}$, the angle between the two gratings was 75°, and the angle between their directions of motion 150° accordingly, background, grating and intersection luminance were 0.5–140 $cd m^{-2}$, the mean stimulus luminance was $\sim 35 cd m^{-2}$ and the duty cycle was 0.3. Two non-pattern-biased and two pattern-biased plaids were constructed: One plaid stimulus (non-pattern-biased 1, NPB 1) was composed of two gratings of different luminance and in a depth-ordered configuration which introduces the strongest component bias, both from the point of view of stimulus construction and perception (Stoner et al., 1990). A second plaid stimulus was composed of two gratings of the same luminance as the darker grating in NPB 1 and low contrast at the intersection (non-pattern-biased 2, NPB 2). The two remaining plaid stimuli were strongly pattern-biased because they were composed of the symmetric (iso-luminant) gratings as NPB 2 but strong contrast at the intersections caused by either very low ('black' intersection, pattern-biased 1, PB 1) or very high luminance ('white', pattern-biased 2, PB 2). The protocol consisted of seven stimuli presented randomly. Four different plaid stimuli with upwards direction of pattern motion, two moving grating stimuli of the same orientation, direction of motion and speed of the plaid components, and one grating stimulus representing the orientation, direction of motion and speed of the pattern direction of the plaid stimulus.

Optical data analysis

Imaging and data analysis were performed as described previously (Schmidt et al., 2006) under N_2O (70%), O_2 (30%) and halothane (0.6%) anesthesia. Plaid maps were calculated as differential maps by dividing maps obtained with plaid stimuli by the sum of maps obtained by the two component stimuli ("component subtractor" which isolates the pattern response of the map) when stimulating separately or by the map obtained with the grating moving in the pattern direction ("pattern subtractor" which isolates the component response of the map) (Figs. 1, 2, 4, and 8A).

The normalized plaid maps (differential response of the division "plaid map / model map") were superimposed on the grating angle maps and plaid specific activation was coded by brightness of the colour in the underlying angle map (Figs. 2 and 4). Further, a response profile of the differential response per pixel after high-pass filtering (scaled to its maximum and minimum and shifted to positive values) was plotted against the orientation preference obtained during stimulation with oriented gratings and categorized into 18 classes of 10°-increments (Figs. 3, 5, and 8B). To compare different data sets, levels of relative activity were normalized and expressed as per cent of the mean relative activity per plaid map (Fig. 6).

To compute component and pattern indices, the differential response maps (e.g. Fig. 1, second and third columns) were spatially correlated with the model map (component model map – sum of the two maps obtained by the two component gratings; pattern model map – obtained by the horizontal grating moving in the pattern direction as illustrated in Fig. 1, first column). Mean pattern and component indices for the four different plaid stimuli were computed by averaging the respective Spearman rank correlation coefficients obtained in all single data sets (Fig. 7).

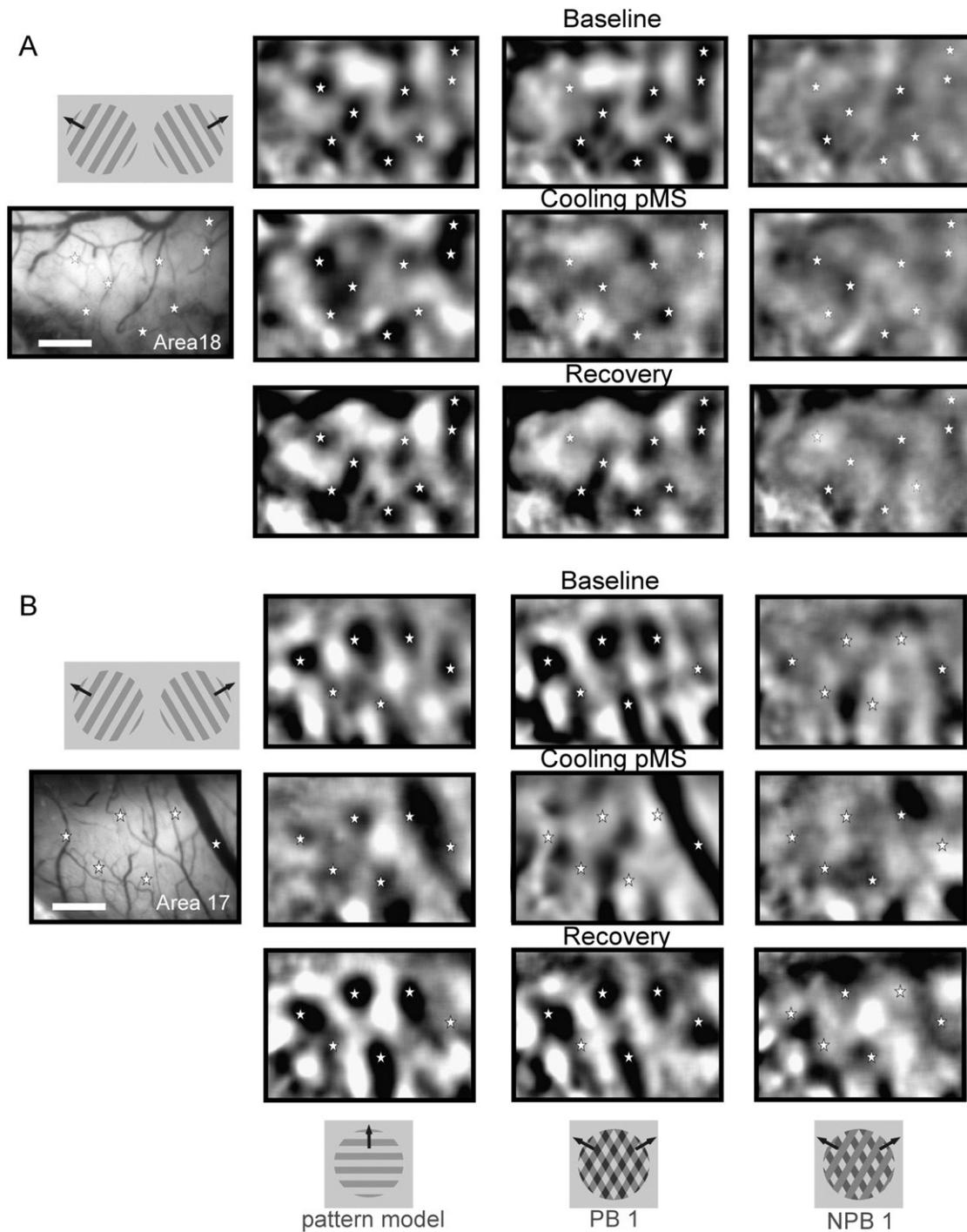


Fig. 1. Differential maps: Maps obtained with a pattern model grating (first column) and upwards moving plaid stimuli (second and third columns) are divided by the summed maps evoked by the two components when presented separately, in area 18 of cat P (A) and in area 17 of cat C (B). Dark colours code for high light absorption. White stars are placed in domains responding to stimulation with a horizontal grating moving upwards (pattern model) under baseline conditions (first column). Note that under baseline condition a strongly pattern-biased plaid (dark intersection luminance, second column), but not the depth-ordered plaid (third column) activates similar domains as the horizontal grating. When pMS cortex was deactivated (cooling) this specific activity ceased for plaids but not for grating stimuli. Pattern-like activity recovered after rewarming. Scale bar: 1 mm. Sketches to the left: normalization procedure. Sketches depict the visual stimulus and apply to the entire column.

Results

Optical imaging of intrinsic signals in areas 17 and 18 was combined with reversible thermal deactivation of posterior middle suprasylvian (pMS) cortex. Visual stimulation consisted of two non-pattern-biased and two more pattern-biased plaids with upwards pattern direction. This set of stimuli was complemented with three

additional stimuli, which were used to calibrate the activation seen with the different plaid stimuli (see Schmidt et al. (2006)). Two of these stimuli were oblique gratings which constituted the two components of the plaid stimuli moving with the same orientation, direction of motion and speed (component model). The third stimulus was a horizontal grating moving upwards with the same speed as the pattern direction of the plaid stimulus (grating pattern model).

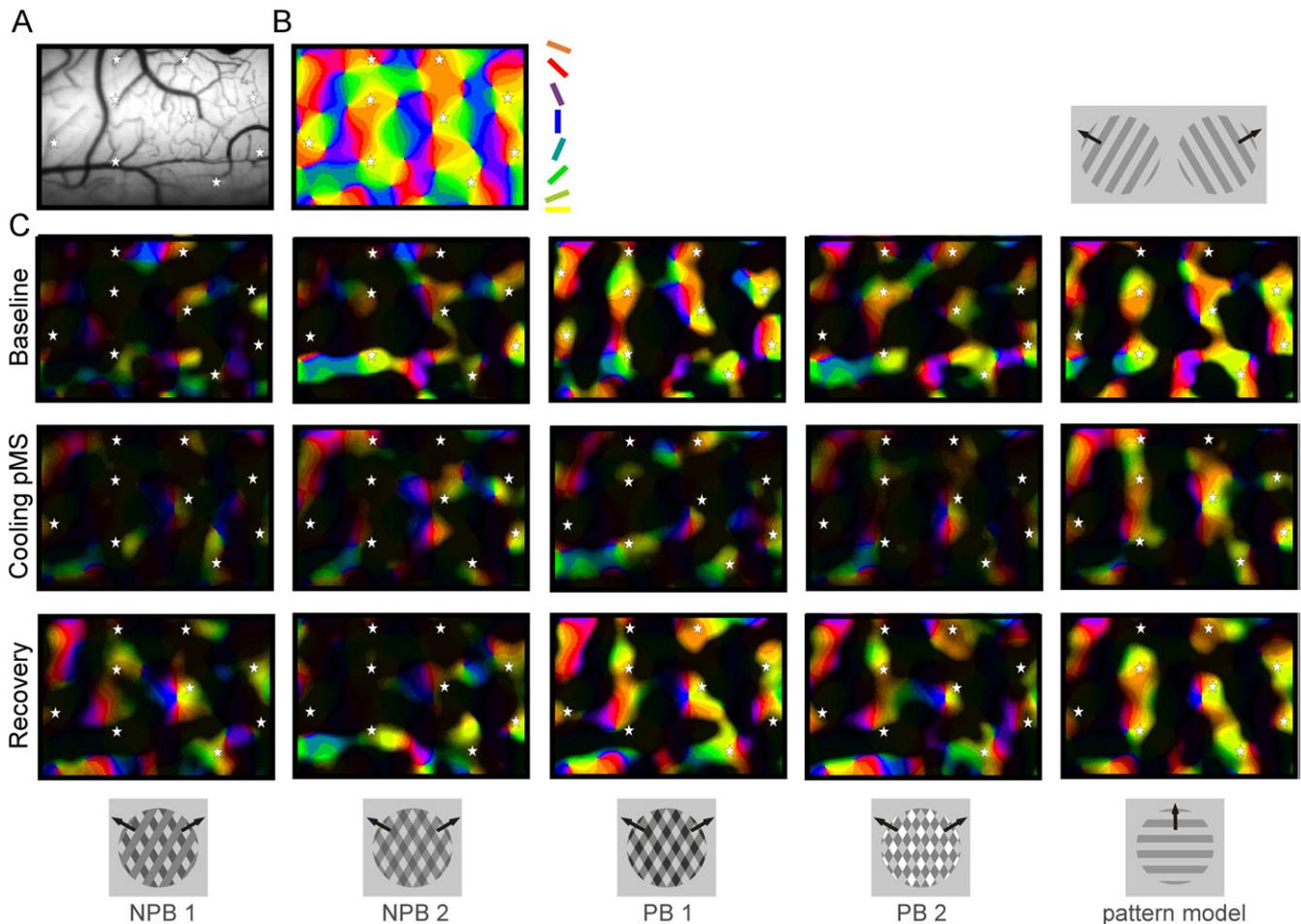


Fig. 2. Maps of pattern-like motion activity in area 18 (cat F). A: Video image of the recorded area. B: A conventional colour-coded orientation map (colour-code according to bars on the right) was obtained by stimulation with square-wave gratings moving in eight different orientations at 16 deg/s and 0.1 c/deg and pixel-wise vectorial addition of the single conditions. C: Plaid and pattern model (horizontal grating) activity maps superimposed on the colour angle map after normalization by the summed component maps. Level of pattern-like motion activity is coded by the colour brightness; bright colours indicate strong activation by the plaid stimulus. Colour-code as in A. Under baseline conditions particularly pattern-biased plaid PB 1 strongly and PB 2 to a lesser extent activate yellow orientation domains driven by horizontal contours (pattern model). This type of activity decreases with MS cooling and recovers with MS rewarming. Note that the structure of the pattern model map on the right is not affected by cooling. Scale bar: 1 mm. Ant: anterior, Lat: lateral. States as indicated on the left.

Plaid stimuli evoke pattern-like activation in areas 17 and 18

In order to extract pattern-like activity in the response, plaid pattern maps were calculated as differential maps. Activity distributions obtained with plaid stimuli were normalized by division to the sum of activities obtained with the two component stimuli when presented separately. This should emphasize any specific activation in the maps not explained by the activity caused by the two stimulus components. Fig. 1 shows such differential maps for the two extreme plaid stimuli, a depth-ordered one with low pattern bias and a plaid with low intersection luminance and high pattern bias. When comparing the maps with the grating moving in the direction of motion of the pattern there is a striking similarity between the map evoked by the strongly pattern-biased plaid (second column) and the respective grating map (first column). This holds for both central area 18 (Fig. 1A) and area 17 (Fig. 1B). The differential map evoked by the depth-ordered plaid is flat in both cases indicating that all activations are basically explained by the sum of the two component gratings (third column).

Pattern-like activations decrease in the absence of transcortical feedback

In order to examine the influence of transcortical feedback on these activity distributions we recorded plaid and model evoked

activities while pMS cortex was thermally deactivated (Fig. 1). This procedure abolished the pattern model-like activity distributions (second column) while the spatial distribution of the activity evoked by the horizontal grating moving upwards remained largely unaffected (first column).

In order to describe the pattern activations for the different plaid stimuli as response profiles within the functional domains of the visual cortex we recorded a conventional grating orientation map from the same region for each data set. Compound maps were computed displaying the pattern specific activity as brightness and the underlying orientation preference as colour (Figs. 2 and 4). As indicated by the differential maps in Fig. 1, the map of the pattern-biased plaid with low intersection luminance (PB 1) peaks in the same orientation domains which are activated by the horizontally oriented and upwards moving grating. In comparison and according to their weaker degree of pattern bias (Stoner et al., 1990) pattern activity evoked by all other plaids is weaker (Fig. 2) or absent (Fig. 4). Thus, the respective compound maps are darker and peak around the vertical orientation domains (blue) jointly activated by the two component gratings. Deactivation of pMS cortex abolished the pattern-like activity distributions present in baselines leaving residual activation mainly in domains responding to component-like motion (Figs. 1, 2 and 4). After rewarming of pMS cortex pattern-like activity distributions recovered (Figs. 2 and 4).

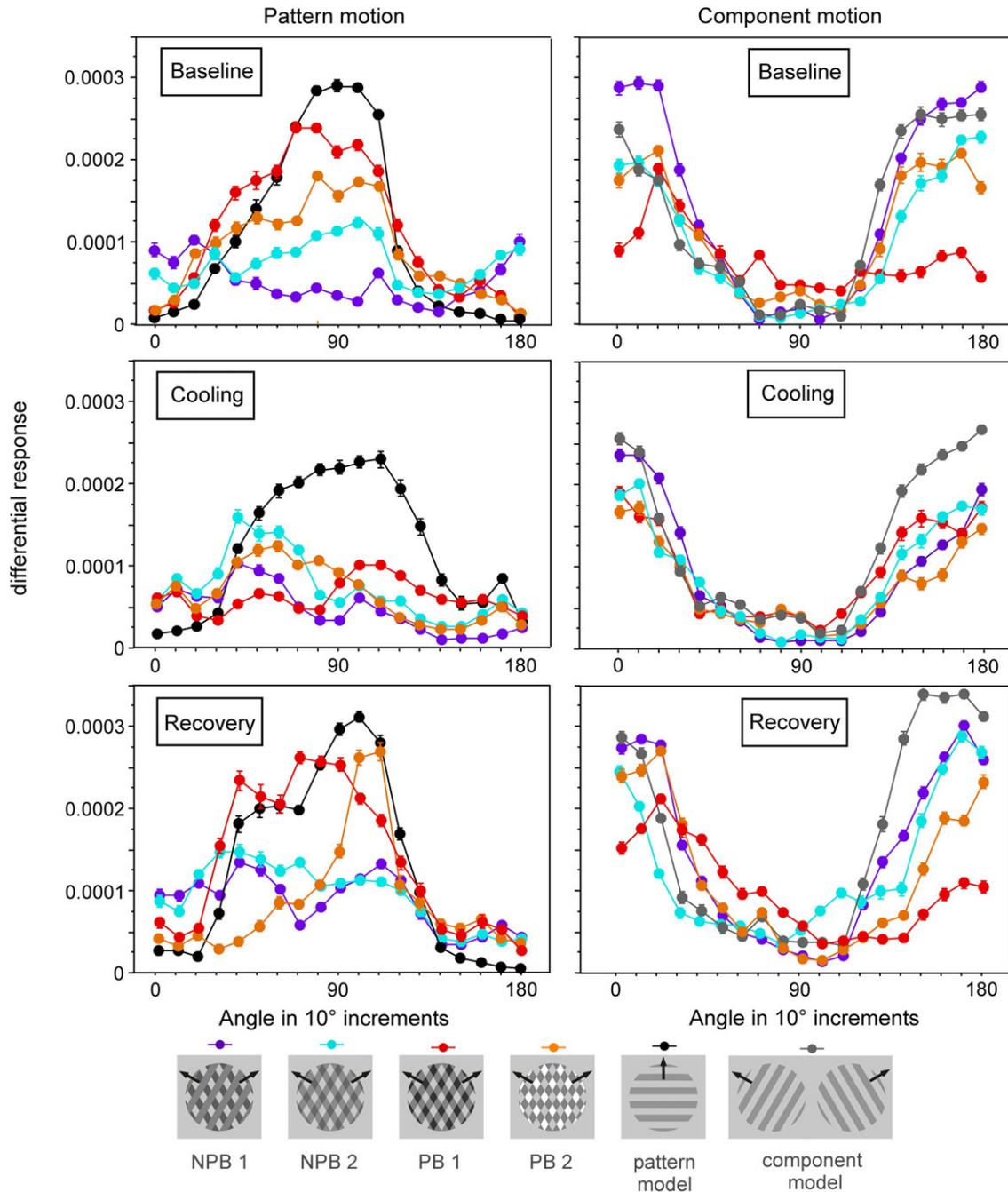


Fig. 3. Differential response profiles for the data set in Fig. 2 (cat F): Relative pattern- and component-like motion activity averaged over pixels within individual orientation compartments during baseline, MS cooling and recovery conditions. Upper value: maximum response, 0: minimum response to pattern motion. Left, component normalized activity yielding pattern-like motion activity; right, pattern normalized activity yielding component-like motion activity. Opposite directions of movement are lumped together in orientation domains. Angular compartments are binned in 10-degree steps. Labels indicate the direction of motion. Even for component-like activity the response gain decreases, however, specific changes can be observed for pattern-like activity. Note that the peak around 90° for three of the four plaid stimuli (red, orange and blue traces) but not for the pattern model itself (black trace) gets abolished during cooling. Error bars: SEM (standard error of the mean of pixels).

Occasionally (see supplementary Fig. 1), plaid stimuli which did not evoke pattern-like activity prior to deactivation transiently showed pattern activity during the recovery phase. Fig. 4 illustrates such a case for area 17 with absent baseline pattern activity for PB 2 and rather strong pattern motion for that plaid in the recovery (PB 2, Figs. 4 and 5).

In 40, 3% of all cases, pattern indices were higher in the recovery than in the baseline. This might be due to rebound phenomena based on temporarily increased feedback activity after prolonged silencing of pMS cortex.

Feedback is crucial for the discrimination between global and local motion imprints

In order to substantiate the above-mentioned findings on a quantitative basis, we computed response profiles of the plaid specific activation by normalizing with the pattern or the component model (Figs. 3 and 5). In these profiles, it becomes obvious that during pMS deactivation the gain of both pattern- and component-like activations decreases but only pattern-like activation disappears (PB 1, PB 2 and NPB 2, cooling). Although component-like activations for all plaid

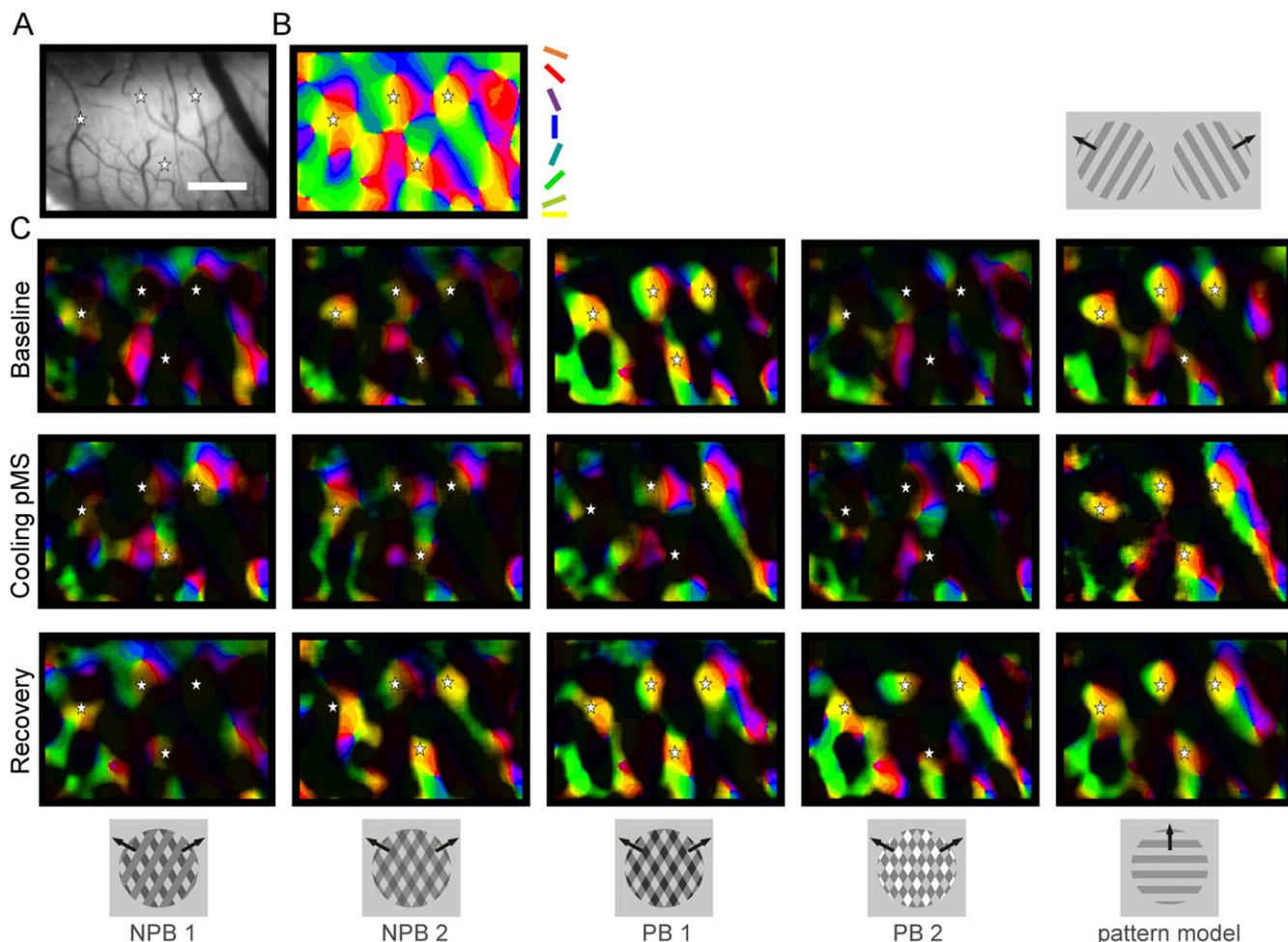


Fig. 4. Maps of pattern-like motion activity in area 17. Same data as in Fig. 1B (cat C). A: Video image of the recorded area. B: A conventional colour-coded orientation map (colour-code according to bars on the right) was obtained by stimulation with square-wave gratings moving in eight different orientations at 4 deg/s and 0.5 c/deg and pixel-wise vectorial addition of the single conditions. C: Plaid and pattern model (horizontal grating) activity maps superimposed on the colour angle map after normalization by the summed component maps. Same conventions as in Fig. 2. Pattern activity present in the baseline for PB 1 vanishes during cooling. In this particular example, pattern-like motion activity is instructed in the recovery for the two other plaid stimuli NPB 1 and PB 2. Note that in the average baseline pattern motion evoked by PB 2 is significantly higher than for NBP 2 (see Fig. 6, and Schmidt et al. (2006)). Scale bar: 1 mm. Ant: anterior, Lat: lateral.

stimuli also decrease, their activity distributions do not change (Figs. 3 and 5, cooling). No obvious or significant differences could be observed between data sets taken from area 17 or area 18. Therefore, response profiles from all data sets were averaged by normalizing them to their respective mean which was then set to 100% (Fig. 6). For statistical evaluation, we separated activity distributions into two angle compartment bins of equal size (compartment P, 45–134° and compartment C, 135–44°) and tested them against each other using a Mann–Whitney U-test (as in Schmidt et al. (2006)). For pattern motion maps (left column of Fig. 6), both plaids PB 1 and PB 2 as well as the pattern model evoke highly significantly more activity in compartment P than in compartment C ($p < 0.0001$) in baseline and recovery conditions. During cooling of pMS cortex, only the pattern model remains significant ($p < 0.0001$). For component motion maps (right column of Fig. 6), we observe highly significantly more activity in compartment C than in compartment P for all stimuli during all baseline, cooling and recovery conditions. Apparently, the specific pattern motion traces evoked by plaid stimuli in primary visual areas vanish during deactivation of pMS cortex while the component motion traces largely remain.

In a next step, we directly compared the different plaid evoked maps with the grating model evoked maps and got a more detailed picture of the effect of deactivating pMS. By correlating plaid pattern

maps with the model maps of exclusive pattern or component activity we obtained a pattern and a component index for each state (Fig. 7). The correlation analysis revealed that, in the individual data sets, high pattern indices were accompanied by low component indices and vice versa. During baseline conditions, average pattern indices were high for both pattern-biased plaids (PB 1 and PB 2) and decreased when deactivating pMS cortex. In concordance, their initially low component indices increased in the absence of feedback. The pattern index decrease was significant for the whole pool of 19×4 (per data set) indices (Wilcoxon, $p < 0.01$). When separating stimuli the decrease was highly significant only for PB 1 as was the increase of the component index for this stimulus. Also, the recoveries of those changes are significant (Wilcoxon, $p < 0.001$).

Effects of graded deactivation of pMS cortex on pattern model and grating response

In order to further examine the specificity of the deactivation effect as opposed to an unspecific gain decrease affecting all responses we performed a graded cooling experiment by first lowering the temperature of the probe down to 12 °C and subsequently down to 1 °C. Cooling only to 12 °C deactivates only the superficial layers of pMS (Payne et al., 1996). Interestingly, we observed only a slight

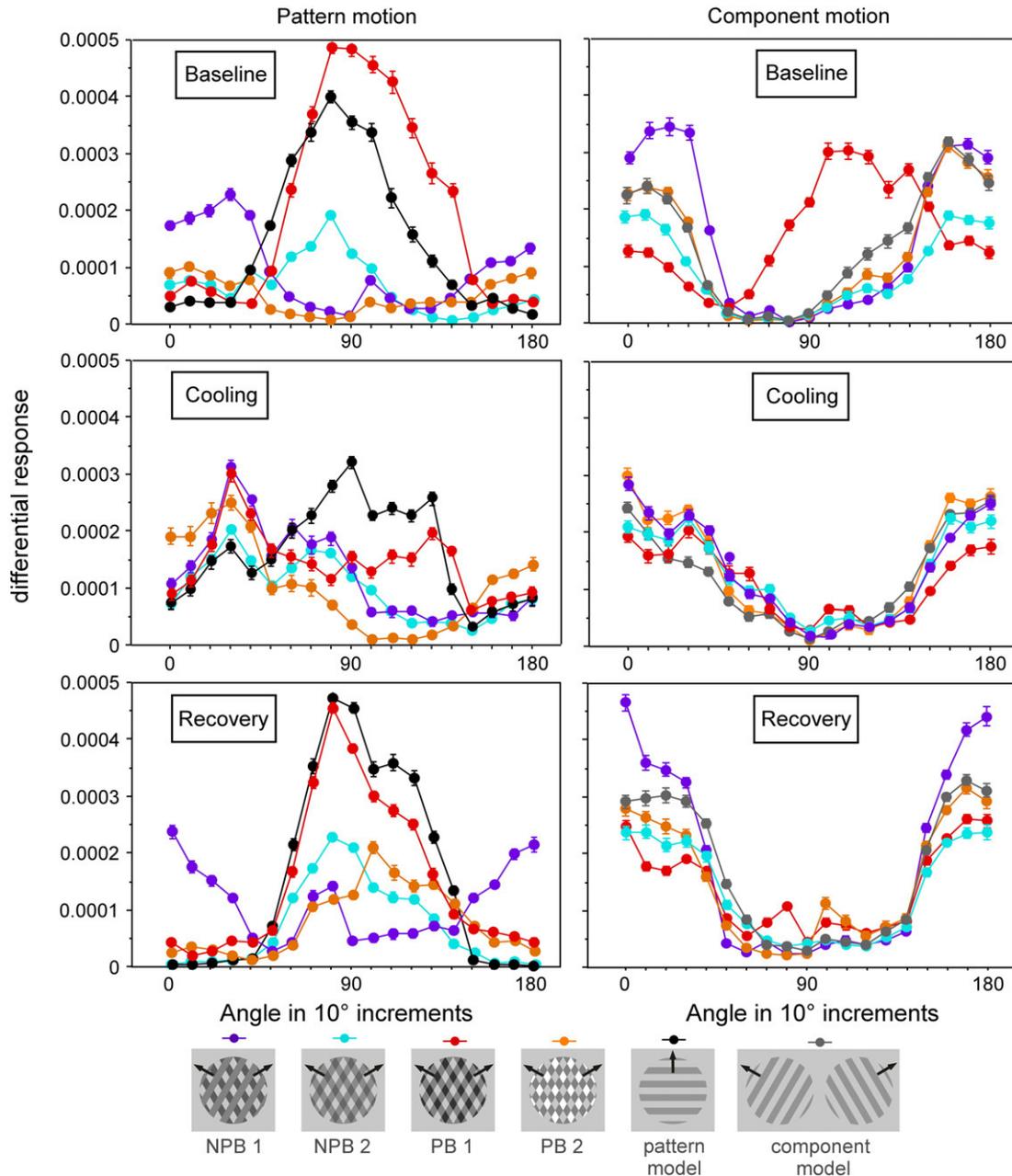


Fig. 5. Differential response profiles for the data set in Figs. 4 and 1B (cat C): Relative pattern- and component-like motion activity within individual orientation compartments during baseline, MS cooling and recovery conditions. Same conventions as in Fig. 3. The peak around 90° for two of the four plaid stimuli (red and blue traces) but not for the pattern model itself (black trace) gets abolished during cooling. Note the rebounding recovery peak for PB 2 (orange) and NBP 1 (violet) which was not present in the baseline.

unspecific lowering of contrast in the images evoked by both grating and plaid stimuli at that temperature (Fig. 8). Only when cooling through the whole cortical thickness the pattern motion-like activity obtained with stimulation with PB 1 disappeared. This holds also true when examining subsequently recorded smaller data blocks of only 8 repetitions demonstrating stability of maps during each of the four different conditions (see supplementary Fig. 2).

Discussion

In summary, our data indicate that representations of global motion strongly decrease and that representations of local motion cues predominate for all plaid stimuli when feedback from MS cortex is deactivated. Therefore, we conclude that particularly global/pattern motion evoked activity in cat areas 17/18 is critically dependent on

these feedback signals. As described previously, deactivation of the middle suprasylvian areas (Galuske et al., 2002; Shen et al., 2006) as well as of other visual areas sending feedback to primary visual cortex (Wang et al., 2000) unspecifically decreases the gain of the responses in primary visual cortex. Accordingly, also the model maps produced by grating stimuli displayed reduced signal strength when removing feedback (Fig. 1). Thus, one function of feedback might be to enhance responses in lower visual areas and serve as a control of contrast gain. Alternatively, the sudden removal of many excitatory inputs through cooling might provoke a temporary unspecific drop in firing thresholds. This is not a contradiction to an additional specific effect. This view is supported by the graded cooling result (Fig. 8). When not cooling the entire thickness of pMS and thus removing only some feedback inputs both plaid and grating responses decrease slightly. Only when cooling all including the strongly back-projecting

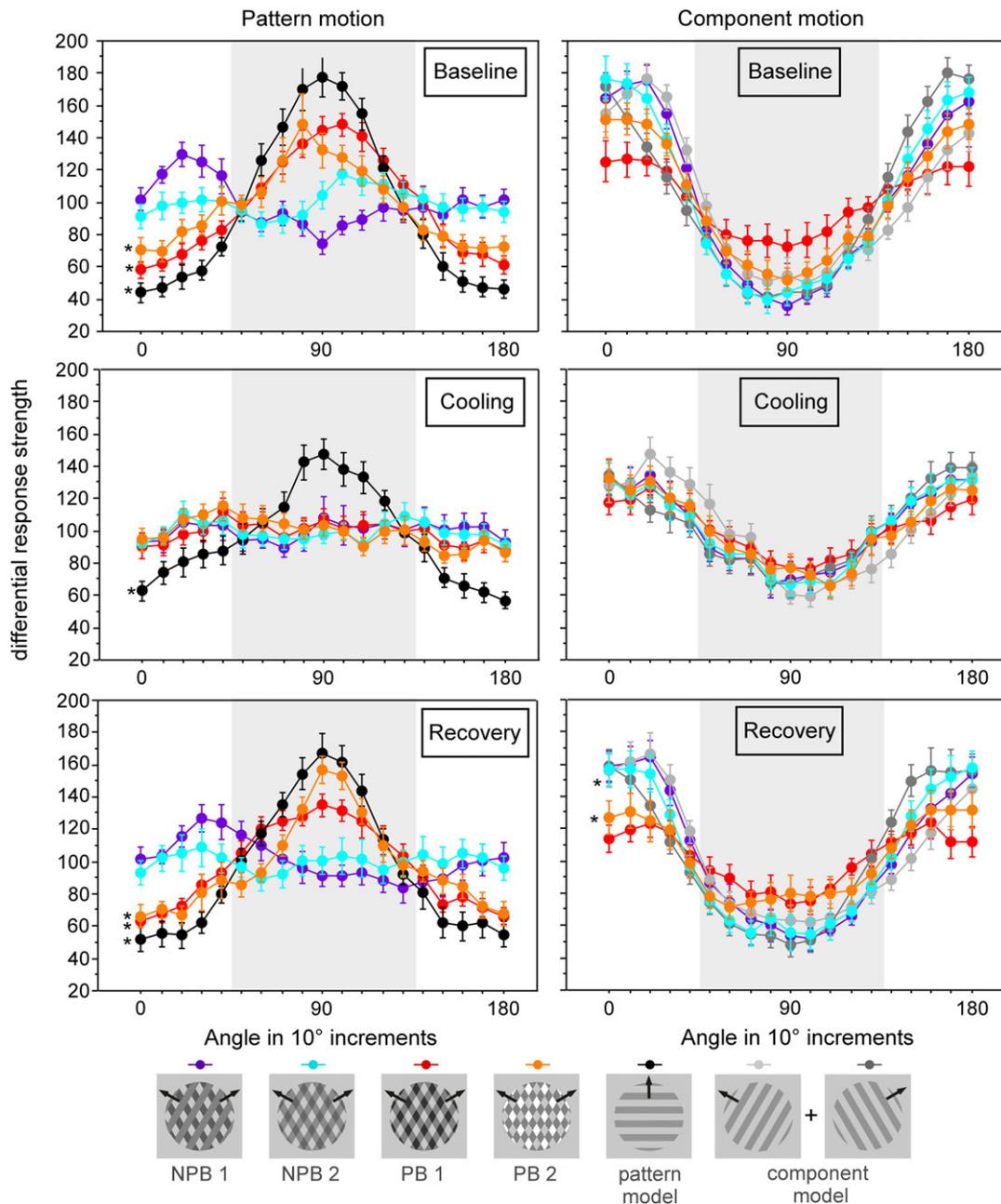


Fig. 6. Differential response profiles for all data sets ($n = 19$) from 6 cats in percentage of the mean activity per plaid evoked map within different angle compartments. Left column: normalized pattern-like activity; right column: normalized component-like activity. Asterisks (only drawn in left column) indicate significant (Mann-Whitney-U, $P < 0.0001$) activity differences in the two angle compartment bins of equal size (grey for the pattern direction of motion: $45\text{--}134^\circ$, white for the component direction of motion: $135\text{--}44^\circ$). Only the black curve (pattern model grating) keeps its shape during cooling. However, note, that component-like activity can be observed throughout all conditions and for all stimuli (all compartment differences in the right column are highly significant).

infragranular layers the pattern activity for the plaid stimulus gets eliminated but the grating response does not decrease any further. Their spatial layout remained unaffected while pattern-like activation in the very same domains was lost completely when stimulated by plaid stimuli while component-like activation even improved for plaid PB 1 (Fig. 7). The overshooting rebound of pattern motion activity in the maps after rewarming MS cortex (see also supplementary Fig. 1) additionally emphasizes that particularly pattern motion was abolished by the removal of feedback. This indicates that different mechanisms support the activation of these domains by oriented gratings or 'pattern-like' plaid stimuli (see also Figs. 6 and 7). In the latter case, the contribution of feedback signals from the infragranular layers of pMS appears to be crucial while in the former case, feedback is not required. This conclusion supports the hypothesis that global or

pattern motion is constructed in a "cascaded" manner (Rust et al., 2006). The single components of composite patterns such as plaids directly activate orientation and direction domains in primary visual cortex via feed forward connections. Pattern motion aspects may be combined at a later processing stage and are fed back to contribute a subthreshold input according to the true global direction of the stimulus. This interpretation is backed by the observation that both local and global directions of motion are represented in areas 17 and 18 (Schmidt et al., 2006).

In the averaged response profiles during cooling, pattern-motion-like traces are significantly lower than component-like traces for both pattern-biased plaids PB 1 and PB 2 (Fig. 6). However, cooling-induced changes of pattern indices for other plaid stimuli than PB 1 do not reach significance, possibly because of low baseline pattern

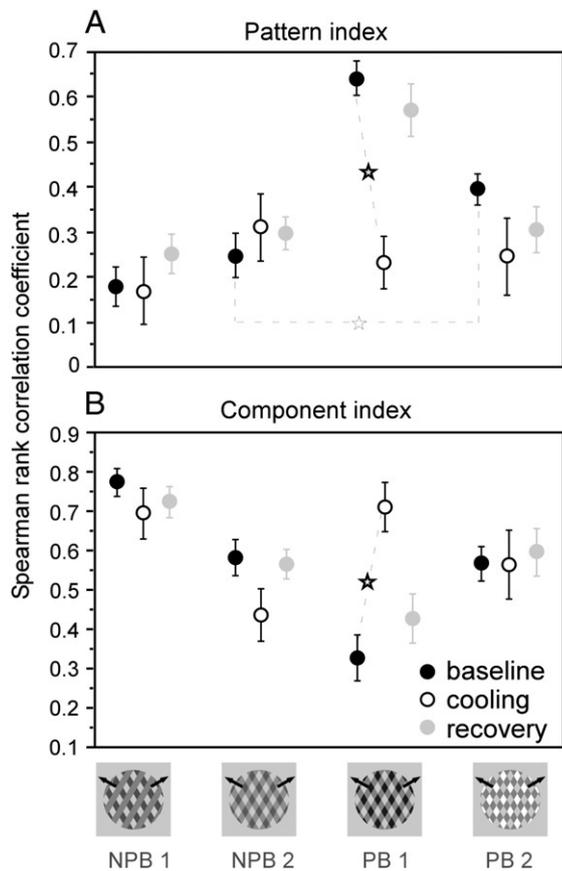


Fig. 7. Mean pattern component indices obtained with different plaid stimuli for all data sets during baseline (filled black dots), MS cooling (unfilled black dots) and recovery (grey dots) conditions. Spearman rank correlation coefficients (y-axis) between plaid maps and the respective component or pattern model maps were computed pixel-wise in a large region of interest. Decrease of the pattern index and increase of the component index of PB 1 in the absence of feedback are significant as are their recoveries (stars, Wilcoxon, $p < 0.001$). Error bars: SEM. Note that baseline pattern indices are significantly higher ($p < 0.01$) for PB 2 than for NPB 1 and 2.

indices. Plaid PB 2 is psychophysically pattern-biased but has lower baseline pattern indices than PB 1 (but not lower than NPB 2, see also Schmidt et al. (2006)). We assume that the inverted background-foreground assignment in case of the white intersections renders it less compatible with transparency and worse in evoking pattern motion than PB 1. Moreover, feedback loops are not fully functional in anesthesia (Pack et al., 2001), thus possibly limiting the range of feedback-driven interpretation for less pattern-biased plaid stimuli. Manipulating feedback connections in this state might eventually bring out pattern motion in the rebound phase which was not visible before (for example, PB 2 and NPB 1 in Figs. 4 and 5).

Anesthesia might be also one of the reasons why the cooling effect for PB 2 is, on average, not significant, namely, because the baseline “pattern state” is not optimal for that plaid.

There is also evidence that cells in cat pMS cortex do not specifically indicate the pattern motion direction of plaid stimuli but only the global motion direction of random dots (Villeneuve et al., 2006). However, it cannot be entirely ruled out that cooling of pMS spread out to the posterior portion of the anterior part of the lateral suprasylvian sulcus (AMLS) where pattern-selective neurons have been found (Ouellette et al., 2004).

There are further motion-sensitive areas even higher in the cortical hierarchy and sending feedback to pMS cortex like the anterior ectosylvian sulcus which have been shown to faithfully signal the true direction of a plaid pattern (Scannell et al., 1996; Zabouri et al., 2008). These areas do not directly project to areas 17 and 18 and deactivation

of the ectosylvian cortex does not directly affect responses in area 18 (Galuske et al., 2002). Finally, our data do not allow us to decide whether MS cortex is the ultimate source of these signals or is itself under feedback control of other higher visual areas which are responsive to the pattern motion direction of plaid stimuli. There may be even motion signals reaching pMS indirectly via feedforward thalamic pathways (e.g. superior colliculus or pulvinar, see below).

Compatible with a motion processing loop feeding pattern selectivity back to areas 17 and 18 is also the result on graded cooling. If the decision about pattern or component motion would involve exclusive processing within pMS one might have expected a specific effect in the feedback receiving areas already when disturbing only the supragranular layers. The infragranular layers do not only send out the majority of the feedback projections to areas 17 and 18 but also to the lateral-posterior pulvinar complex (LP, Payne and Lomber, 2003; Huppé-Gourgues et al., 2006). LP is reciprocally connected with AEV (Mucke et al., 1982; Norita et al., 1986). Further, it contains itself plaid pattern-selective neurons (Merabet et al., 1998) and projects to area 18 and pMS (Payne and Lomber, 2003). Removing AEV alone did not eliminate pattern selectivity in LP but additional removal of pMS did (Merabet et al., 1998). In this sense, removing with pMS (including its infragranular layers) a key part of an extrastriate motion processing loop might be finally sufficient to eliminate also the traces of pattern-motion-like activity in areas 17 and 18.

Based on its connectivity cat pMS cortex was considered to be a homologue of monkey/human area MT (Payne, 1993). Therefore, support for a critical role of posterior MS cortex in pattern processing can be also deduced from primate studies. Pattern motion selective single cells have been found in V1 of the awake monkey and it was proposed that pattern motion selectivity is fed back from MT to V1 (Guo et al., 2004). Interestingly, we see pattern motion imprints in area 17 even in the anesthetized animal and these imprints disappear when deactivating the higher visual area. This gives reason to assume that the type of feedback signal we observe operates mainly on a subthreshold level, as pattern motion selective spiking neurons are usually found in awake recordings (Pack et al., 2001; Guo et al., 2004). This interpretation is supported by previous evidence that brain imaging techniques reveal synaptic processes that are hardly detectable in spiking activity (Logothetis et al., 2001; Schmidt et al., 2004, 2006; Niessing et al., 2005) but might reflect local computations driven by feedback and partly thus explain our finding.

Recent anatomical evidence points increasingly towards feedback connections to V1 as an important cortical circuit which could mediate long range influences of visual context from outside the classical receptive field (Angelucci et al., 2002; Angelucci and Bullier, 2003). In monkeys, it has been shown that MT feedback can modulate spatial integration in V1 (Hupé et al., 1998; Supér and Lamme, 2007). Here, we demonstrate that feedback is specifically involved in the differentiation between the local and global directions of motion. Taken together, these findings support the view that feedback connections play an instructive role in visual processing.

Models based on psychophysical observations of a fast high-level categorization in visual sceneries have led to a reverse-hierarchy-theory (Hochstein and Ahissar, 2005). According to this theory feedback projections provide information about features of a larger area of visual field than those directly accessible by the early receptive fields. This can only happen after these features have been processed in a higher visual area which then guides a later stage low-level vision of the details. This type of processing may well be exemplified in the present study. It is highly likely that the early receptive fields giving rise to the activity maps we describe do not cover two intersections and thus do not have the information about the pattern direction of motion. Nevertheless, the global aspects of the plaids stimuli – which are ambiguous – can be observed in the feedback supported subthreshold activity. A function of this feedback could be to flexibly

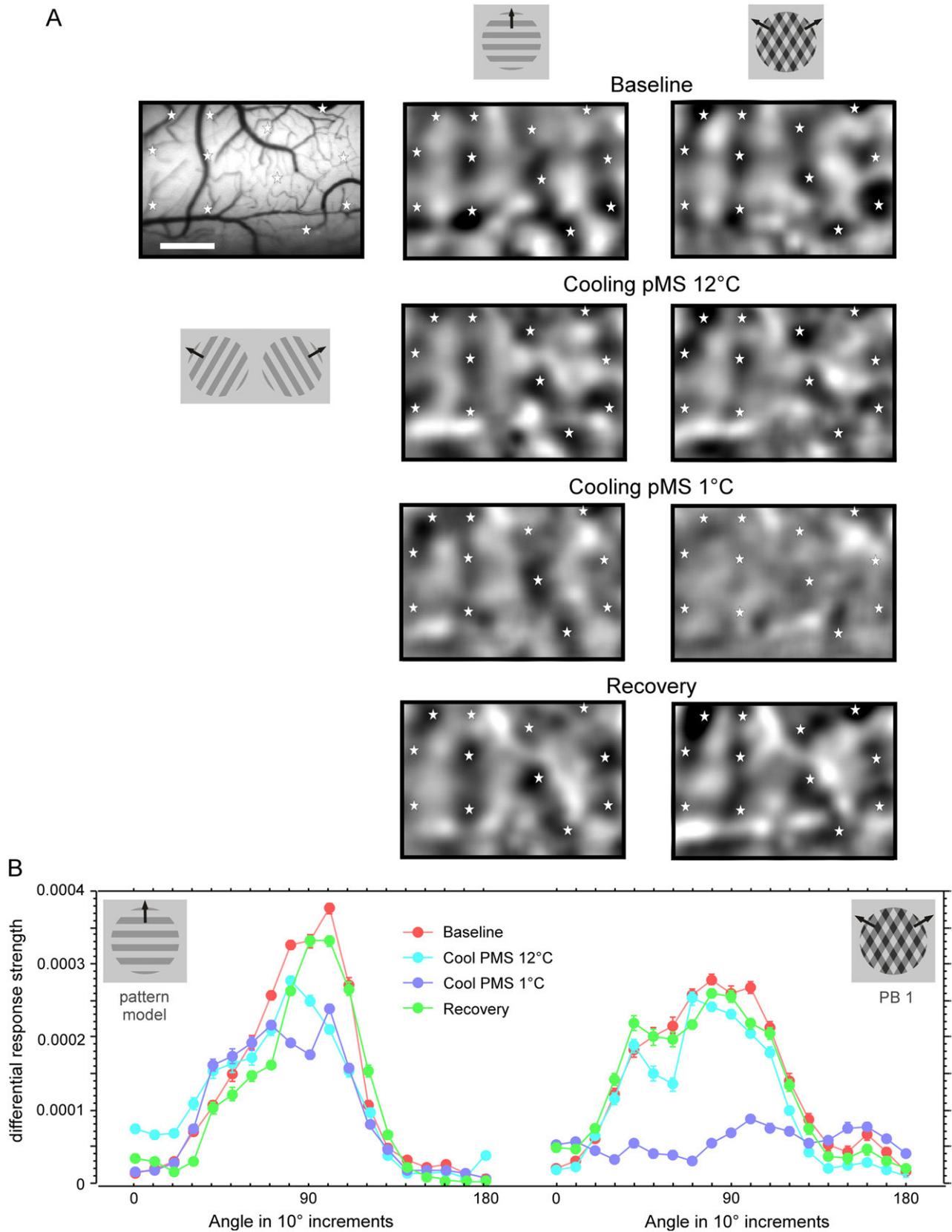


Fig. 8. Effect of graded cooling of pMS cortex, same area 18 recording site as in Fig. 2 (cat F): A: Differential maps (as in Fig. 1) obtained with a pattern model grating (first column) and upwards moving plaid stimuli (second column) are divided by the summed maps evoked by the two components when presented separately. When pMS cortex was deactivated only partly (12 °C) activity decreased only slightly and unspecifically for both plaid and grating (second row). Only with complete deactivation (1 °C) pattern-like activity evoked by the plaids ceased but the structure of the grating map remained (third row). Specifications as in Fig. 1. B: Differential response profiles (as in Fig. 3) of the data shown in A. Baseline, recovery and different cooling temperatures are differently coloured (see legend). Note that the peak around 90° for PB 1 vanishes only when cooling the entire thickness of pMS (dark blue line).

tune the bias for pattern motion by intersection processing within the feedback loop and enhance the gain for pattern motion activity in V1 as a top-down instruction when appropriate.

Supplementary data to this article can be found online at doi:10.1016/j.neuroimage.2010.08.017.

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