syrinx, in which the right side tends to generate frequencies 0.5-1.0 kHz higher than the left. Thus, the regression line relating fundamental frequency to EMG activity is shifted to the right, so that at any amplitude of EMG the fundamental frequency of the right syrinx is 0.5-1.0 kHz higher than that in the left syrinx. This selective expression of bilateral motor patterns by unilateral gating in brown thrashers presents a novel mechanism for neural lateralization. It can also explain the paradox of highly asymmetrical song production in the absence of hemispheric differences in the size, neuronal structure10,11 or activity12,13 of the song control nuclei in other songbirds16. Bilateral activity of the non-gating muscles may stabilize the carillarginous framework and prent the silent side to allow rapid switching between the two sides, accounting for bilateral central motor activity during asymmetrical sound generation12,13,14. Thus, lateralization of song production may have evolved to increase the spectral and temporal complexity of signals used in vocal communication. Conventional hypotheses explaining song lateralization as a means of achieving a unified control centre or to free brain space for other tasks, such as additional memory15,16 need to be re-evaluated.

Visual attention modulates metacortex masking

V. S. Ramachandran & S. Cobb

Brain and Perception Laboratory, Center for Research on Brain and Cognition, 0109, University of California at San Diego, La Jolla, California 92039-0109, USA

How does the human visual system 'bind' different fragments in the visual scene to create enduring representations of objects? A visual illusion known as 'metacortex'9 or backward masking provides compelling evidence that perception is not instantaneous and that it occurs sequentially in distinct stages. If a solid white target square is displayed for 50 ms in a tachistoscope, switched off, and followed by a 50 ms display of two flanking mask squares, remarkably, subjects report seeing only the two flanking squares: the first square is simply not 'seen'. By plotting the magnitude of masking as a function of the delay between the target and mask (the stimulus onset asynchrony), one can obtain a characteristic 'U'-shaped function with optimum masking occurring at about 50 ms, and no masking with synchronous target and mask presentations or at delays higher than 300 ms. The illusion is also highly sensitive to the dimensions of the stimulus such as colour, orientation and spatial frequency, and it has been suggested that it is based on 'low level' autonomous visual mechanisms rather than cognitive processes. Here we describe a novel visual stimulus that demonstrates that metacortex can be strongly modulated by 'top down' influences such as voluntary visual attention.

Our stimulus sequence was identical to a standard metacortex display (Fig. 1a) except that our central target was a disk rather than a square. The target disk (a) in Fig. 1b was presented for 100 ms in frame 1 and followed by two flanking squares (s) that appeared in frame 2 for another 100 ms. This caused a complete erasure of the target from consciousness. We then added two additional disks in frame 1 (Fig. 1b), one adjacent to the target (b) and a second one (c) off to one corner of the screen. The stimulus duration and the stimulus onset asynchrony (SOA) (both 100 ms) were longer than in the standard metacortex display. This stimulus sequence was cycled continuously with a long inter-cycle interval of 700 ms. While viewing this display, we noticed that masking of the target (a in Fig. 1b) occurred as expected when we perceptually 'grouped' the two extraneous disks (b) and (c). But we found that if we now grouped target (a) and disk (b) instead, the masking no longer occurred: the target became clearly visible. To confirm this observation, we asked four subjects to view this display and to group perceptually either target (a) and disk (b) or disks (b) and (c) (on different trials) and to rate the vividness and clarity of the target on a scale of 0-5 in relation to the flanking squares while we varied the SOA. A characteristic U-shaped metacortex masking function (Fig. 2) was obtained, but masking was reduced considerably when the subjects grouped the two disks (a) and (b) instead of (b) and (c). This difference between the two conditions disappears if the delay between target and mask is either too long or too short (the two sides of the 'U') suggesting that the effect arises from an interaction between backward masking and visual attention rather than from either alone. We may conclude, therefore, that when visual attention is used to bind the target disk with adjacent features in the image, masking is reduced considerably.

In our second experiment the stimulus sequence was again similar to a standard metacortex display, except that the two new disks appeared at the same time as the central target, one on either side of it, and two new squares appeared at the same time as the flanking mask squares (Fig. 3). The stimuli were cycled continuously with an interval of 700 ms interposed between successive target-mask sequences. In this display, when we attended to the vertical column of squares, the middle disk (the target) was masked vividly, as expected, but when we attended to the horizontal row, the masking was reduced considerably, so that three disks were seen instead of two. By voluntarily switching attention from vertical column to horizontal row, we could make the target disk disappear and reappear at will.

An alternative view of metacortex is that it arises in close association with the apparent motion7 between the target and mask, that is, the mechanism of apparent motion that extracts the motion signal after both stimuli have been displayed does not allow the first stimulus to be recognized as a separate event (as the same object cannot be at two places at the same time).

Because voluntary attention is known to modulate long-range apparent motion14, it is conceivable that it reduces backward masking as well. In our experiment, the attention-based binding of the target with other disks in frame 1 might reduce the strength of the motion signal from the target to the flanking masks, thereby also reducing the strength of metacortex mask-

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FIG. 1 a. Standard metacoronal display. The target (a: depicted as light grey) was followed by the two flanking squares (s: depicted as black), causing a complete erasure or 'masking' of the target. The effect is not seen if (a) and (s) are presented simultaneously. Both target and mask were white in the actual display. b. Modified display used to demonstrate the effect of attention and perceptual grouping on metacoronal. The display is similar to a, except that the target is a disk rather than a square. Also, two new disks, (b) and (c), were displayed simultaneously with the target. The masking squares (s) subtended 0.5° each and the diameter of the disks was also 0.5°. The outer margin of the target disk (a) coincided spatially with the lower margin of the upper square and upper margin of the lower square. Disks (a) and (b) were 0.8° apart (centre to centre) and disk (c) was 2° away from the target, towards the corner of the display. The durations of both target and mask were 100 ms, SOA was 125 ms. To minimize eye movements, the subject was asked always to fixate on a small cross.

FIG. 2 Modulation of masking by visual attention. Durations of both target and mask were 100 ms. On any given trial, SOA was randomly chosen to be one of 6 different values. On different trials, the subject had to ‘group’ either (a) and (b), or (b) and (c) of Fig. 1b, and rate the perceptual clarity of the target (a) on a scale of 0 to 5 (0, invisible; 5, perfectly clear). Trials on which (a) and (b) were grouped were interleaved with trials in which (b) and (c) were grouped. On any given trial and target–mask sequence was followed by a long delay of 600 ms before repeating the same sequence and the stimulus was cycled continuously. This gave the subject enough time to group the disks. No time limit was specified but the subject was encouraged to respond quickly (typically 4 or 5 cycles were required to make a confident judgement). Each data point is based on 24 trials (6 subjects, 4 trials each). The square symbols (■) depict the masking when subjects grouped (b) and (c) and the circular symbols (○) when they grouped (a) and (b). Note the striking reduction in masking when (a) and (b) were grouped at intermediate SOAs and the absence of a difference in masking strength when the SOA was either zero or larger than 160 ms.

FIG. 3 The display used in experiment 2. In frame 1 we displayed a horizontal row of three white disks and in frame 2 there was a vertical column of four white squares. Paying attention to the mask (the vertical column) caused the central target to disappear, but attending to the horizontal row caused the central disk to become unmasked so that three discs were seen instead of two. We used this display to test five subjects (including the two authors). The squares subtended 0.5° each and the stimulus duration and SOA were 100 ms and 116 ms, respectively. The long inter-cycle interval between successive target–mask pairs was 700 ms. In any given trial, the subject was initially instructed to pay attention to the vertical column of figures, and to rate the clarity of the central disk on a scale of 0–5 (0, invisible; 5, clearly visible). He was not given a time limit but was encouraged to respond quickly. The process was repeated while the subject attended to the horizontal row. We also randomly varied the colour of the display so that on different trials all figures were a light desaturated pink, green, or white. This procedure had no noticeable effect on the illusion but it conveyed the impression to the three naive subjects that we were varying something. On 50% of trials the target followed the mask instead of preceding it. The mean ratings for horizontal and vertical were 4.08 and 1.17, respectively (n = 180; 5 subjects x 36 trials). The ratings for the forward masking condition were 4.6 (horizontal) and 4.02 (vertical). This confirmed our preliminary observation that masking is reduced considerably when the subject attends to the horizontal row even though the physical stimulus remains unchanged. The effect of attention could be seen for both backward and forward masking but is much more pronounced for the former.
ing. Indeed, our subjects reported that in the display illustrated in Fig. 1b the target (a) could sometimes be seen 'splitting' into the two masking squares, despite the shape difference (even though the target itself was rendered invisible) but that this splitting did not occur if target (a) was grouped perceptually with disk (b).

When discrete stimuli excite the retina in rapid temporal and spatial proximity, decisions have to be made by a neural network about both the direction of motion and the object identity, with the latter process leading to metacoast. One would expect, therefore, that although apparent motion and metacoast are not identical, they should nonetheless be closely linked, and may be sensitive to the same temporal and spatial parameters. To explore this link more directly, we designed a new display (Fig. 4a) in which frame 1 contained two extra squares that appeared adjacent (in space) to the two masking squares that followed in frame 2. Because of their proximity and shape similarity, subjects now saw vivid apparent horizontal motion between the square in frame 1 and those in frame 2. This reduced the tendency to see the target disc splitting and also reduced backward masking, considerably (see Fig. 4b legend).

These results show that far from being an autonomous front end visual process, backward masking can be strongly modulated by top-down influences such as voluntary visual attention. The effect we have observed may therefore provide a new way of linking attention, motion perception and immediate memory and the technique may also lend itself to physiological experiments on visual attention.12,17

Note added in proof: Unmasking by voluntary attention, at long SOAs, was especially salient with Fig. 1b, but could occasionally be observed if the two extraneous disks (b and c) were deleted so as to exclude perceptual grouping.

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Incorporation of subgenomic amounts of DNA as compensation for mutational load in a gynogenetic fish

Manfred Schartl, Indrajit Nanda, Ingo Schlupe, Brigitta Wilde, Jörg T. Epplen, Michael Schmid & Jakob Parzefall

* Physiologische Chemie I and F Institut für Humangenetik, Biozentrum der Universität, Am Hubland, D-97074 Würzburg, Germany
† Zoologisches Institut and Zoologisches Museum der Universität, Martin-Luther-King-Platz 3, D-20146 Hamburg, Germany
§ Molekulare Humangenetik der Ruhr-Universität, D-44995 Bochum, Germany

A CENTRAL paradigm in evolutionary biology is that sexual reproduction is advantageous over asexual reproduction. One of the long-term disadvantages asexual forms have to face is Muller’s ratchet. In the absence of recombination, theoretically no genotype can ever produce offspring with fewer mutations than its own load. The accumulation of deleterious mutations and gene combinations that cannot be purged should lead to extinction of parthenogenetic forms within 10^5-10^6 generations. Evidence is accumulating, however, that some of these might have survived for such periods or even longer. In the Amazon Molly fish Poecilia formosa we have detected a process that appears to compensate for disadvantages of asexuality, namely incorporation of subgenomic amounts of DNA from a bisexual host species by microchromosomes.