Low-level motor inhibition in children: Evidence from the negative compatibility effect

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ABSTRACT

The masked prime task was used to investigate low-level inhibitory motor control processes in two groups of children (7-8 years and 11-12 years) and in older adolescents/young adults (16-23 years). Masked prime stimuli, presented below the level of conscious awareness, systematically affected reaction times (RTs) to subsequent supraliminal target stimuli: RTs were longer when prime and target were mapped to the same response than when they were mapped to different responses. This negative compatibility effect did not differ significantly between age groups, consistent with the hypothesis that the underlying low-level inhibition processes are already fully developed in children as young as seven years of age. In contrast, performance differences between response repetition and response alternation trials were significantly larger in children, consistent with the hypothesis that higher-level control processes are less effective in children. Results provide converging evidence that whereas the latter processes are mediated by late-maturing (prefrontal cortical) areas, the former processes are mediated by earlier-maturing (possibly subcortical) structures.

INTRODUCTION

Voluntary and automatic inhibitory control

In an ever-changing and potentially dangerous environment, the survival of an organism depends to a large extent on its ability to quickly detect environmental changes and to rapidly respond to them by suppressing any ongoing activity in favour of a more appropriate one. Traditionally, this capacity for inhibitory control has been studied in the context of voluntary response inhibition, for example, in the stop-signal or the go/nogo paradigm, where participants are required to withhold a prepotent response tendency when presented with a particular stimulus. In these studies, evidence has been obtained to suggest that such voluntary, high-level response inhibition relies on control mechanisms in anterior (in particular prefrontal) cortical areas (for overviews, see Band & van Boxtel, 1999; Faw, 2003). Unsurprisingly, there is a close relationship between brain development and the development of voluntary inhibitory control functions: The frontal cortex has the slowest maturation rate of all brain structures, and is subject to developmental changes from childhood until well into adolescence (e.g., Dempster, 1992; Harnishfeger & Bjorklund, 1994; for a review, see Casey, Durston, & Fossella, 2001). Correspondingly, the ability to voluntarily inhibit prepotent response tendencies has been found to improve substantially with age during childhood and adolescence (e.g., Brocki & Bohlin, 2004; Leon-Carrion, Garcia-Orza, & Perez-Santamaria, 2004; Ridderinkhof & van der Molen, 1995).

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However, voluntary inhibition is not the only form of behavioural control. For example, many simple, everyday activities (e.g., scanning a visual scene) require large numbers of similar – but not identical – movements. Therefore, automatic inhibition of the movement that has just been executed in favour of one of the alternatives would prevent perseveration and thus increase efficiency. A classical example of such a non-voluntary inhibitory mechanism is the so-called Inhibition of Return (IOR) phenomenon, where orienting and responding towards a spatial location is impaired if attention has just been removed from this location (Klein, 2000; Maylor, 1985). This kind of inhibitory control is assumed to be mediated by subcortical structures, specifically by the superior colliculus (see Klein, 2000, for an overview). This structure, in contrast to cortical (frontal) areas, matures very early during brain development. Correspondingly, IOR has been observed not only in adults, but also in children and infants (Clohessy, Posner, Rothbart, & Vecera, 1991; MacPherson, Klein, & Moore, 2003; Richards, 2000). Interestingly, when comparing the development of strategic and automatic control processes, MacPherson et al. (2003) found that children between five and ten years of age showed IOR when their attention was exogenously removed from the initially attended location, but not when they had to shift attention endogenously. This is in line with the notion of subcortically mediated (early maturing) automatic control and cortically mediated (late maturing) strategic control processes.

Automatic inhibitory control would also be beneficial under conditions where voluntary control mechanisms are not only impractical, but impossible. Many potentially relevant changes in the environment are too quick or too subtle to be consciously perceived. It is well known that such 'subliminal' stimuli can nevertheless activate a motor response (e.g., Dehaene et al., 1998; Neumann & Klotz, 1994). The question is whether subliminally triggered responses are also subject to inhibitory control. In fact, it has often been argued that response inhibition depends on the conscious detection of task-relevant signals, and thus is not available with subliminal stimulation. Studies of inhibitory control comparing subliminal and supraliminal presentation conditions have generally confirmed this hypothesis (e.g. Allport, Tipper, & Chmiel, 1985; Marcel, 1980; McCormick, 1997; Merikle, Joordens, & Stolz, 1995; Neill, Valdez, & Terry, 1995): Although automatic activation processes were observed with both types of stimuli, evidence for response inhibition was found only with supraliminal stimuli. This led to the conclusion that subliminally presented stimuli can trigger only (pas-sive) activation, and that for active inhibition to occur, stimuli have to be presented supraliminally.

These experiments, however, only investigated voluntary or strategic inhibitory control processes – it is easy to see why these might not be operative when the relevant stimulus has not been consciously perceived. In contrast, recent experiments, employing the masked prime paradigm, have provided evidence for the existence of a low-level, automatic inhibitory control process, which operates independently of voluntary inhibition mechanisms, and appears to be mediated by subcortical (in particular, basal ganglia and thalamic) structures (see Eimer & Schlaghecken, 2003, for an overview). Relative to the neocortex, and specifically to the frontal lobes, these structures mature early, and appear to be already well developed by approximately four years of age (e.g., Mukherjee et al., 2002). Consequently, one would expect children above this age to show well-developed automatic inhibitory control, similar to the IOR findings reported above. However, whereas low-level inhibitory control has been extensively studied in young adults, and is now also being studied in older adults (Schlaghecken & Maylor, 2005; Seiss & Praamstra, 2004), no study has as yet investigated these processes in children. The present study was designed to close this gap.

Using the masked prime paradigm, effects of low-level (priming) and of high-level (strategic) inhibitory control in two groups of children (7-8 and 11-12 years of age) were compared with effects in older adolescents/young adults (16-23 years of age). It was expected that whereas high-level inhibition effects should show clear age-related changes, low-level inhibition effects should be similar in children and adults.

The NCE and low-level inhibition

In the masked prime paradigm, a target stimulus is preceded by a backward-masked visual prime stimulus. Both primes and targets are simple geometrical figures, for example, open arrowheads pointing to the left or right (e.g., '<<' or '>>'). Primes are presented very briefly (usually for only 17 or 33 ms), and are replaced immediately by a larger masking stimulus, presented at the same location for 100 ms. In some experiments, targets are presented simultaneously with the mask; in others, they are presented some time after mask offset. Participants have to make a speeded 2-alternative choice response to the target, for example, a left key-press in response to an arrow pointing to the left, and a right key-press in response to an arrow pointing to the right. On any given trial, prime and target can

be mapped to the same response (compatible trial) or to different responses (incompatible trial), or the prime can be a stimulus that never occurs as a target and, thus, is not mapped to any response (neutral trial). Because of the visual backward masking, prime stimuli are presented below the threshold of conscious awareness, as evidenced by chance level accuracy in numerous prime identification tasks (Eimer & Schlaghecken, 1998, 2002; Klapp & Hinkley, 2002; Schlaghecken & Eimer, 1997). Despite this, primes systematically affect motor responses to the subsequent supraliminal targets, with the direction of these priming effects depending on the interval between masked prime and target. When targets follow the masked primes immediately (mask-target stimulus onset asynchrony [SOA] of 0 ms), positive compatibility effects (PCEs) occur, where performance is facilitated on compatible trials, and impaired on incompatible trials, relative to neutral trials (Aron et al., 2003; Eimer, 1999; Schlaghecken & Eimer, 1997, 2000). With increasing mask-target SOA, however, PCEs diminish and turn into negative compatibility effects (NCEs), with performance benefits on incompatible trials, and costs on compatible trials, at mask-target SOAs of 100 ms or more (Aron et al., 2003; Eimer, 1999; Eimer & Schlaghecken, 1998, 2001, 2002; Klapp & Haas, 2005; Klapp & Hinkley, 2002; Schlaghecken & Eimer, 1997, 2000, 2001, 2002, 2004b; Schlaghecken, Münchau, Bloem, Rothwell, & Eimer, 2003; Seiss & Praamstra, 2004).

These effects seem to originate within the perceptuo-motor control system, rather than reflecting perceptual or cognitive-semantic processes (Eimer, 1999; Eimer & Schlaghecken, 1998; Eimer, Schubö, & Schlaghecken, 2002; Schlaghecken & Eimer, 2000). In fact, electrophysiological and haemodynamic evidence (e.g., Aron et al., 2003; Dehaene et al., 1998; Eimer, 1999; Eimer & Schlaghecken, 1998; Leuthold & Kopp, 1998; Praamstra & Seiss, 2005; Seiss & Praamstra, 2004) indicates that the masked prime activates its corresponding motor response, which in turn increases inhibition of the competing response alternative. When the target is presented immediately after the prime (mask-target SOA of 0 ms), target-related motor processes will begin during this initial prime-related activation phase. Because the prime activated the correct response on compatible trials, but the incorrect response on incompatible trials, the target-related activity will be correspondingly facilitated (on compatible trials) or impaired (on incompatible trials), reflected in behavioural PCEs. However, the duration of this initial activation phase is cut short by the presentation of the masking stimulus. Because a successful mask removes the prime's neural

representation,[1] the initially primed response is no longer supported by corresponding unequivocal input from the perceptual system. It is assumed that this sudden lack of supporting perceptual evidence triggers an active self-inhibition process, which suppresses the initially primed response and, consequently, releases its competitor from inhibition (Bowman, Schlaghecken, & Eimer, in press; Eimer & Schlaghecken, 1998; Schlaghecken & Eimer, 2002). Therefore, with a mask-target SOA of approximately 100 ms, target-related motor responses occur during a phase where activation levels of the initially primed response are reduced, and activation levels of the alternative response are relatively higher, reflected in the NCE.[2]

Response repetition costs and high-level inhibition

In terms of high-level or strategic inhibitory control, it is worth noting that in the masked prime task, repeating a response on successive trials usually results in longer reaction times (RTs) than alternating the response ('repetition costs'). Although the reversed pattern ('repetition benefits') is more common, repetition costs have been obtained in a number of different paradigms (for an overview, see Kleinsorge, 1999). The mechanisms underlying this effect in the masked prime paradigm are currently under investigation, but the following observations have been made (Schlaghecken, unpublished data): First, there is no interaction between response repetition and masked priming, that is, priming effects of equal size are obtained on response repetition and on response alternation trials. Second, repetition costs are obtained under NCE conditions as well as under PCE conditions. In particular, repetition costs tend to be even larger under PCE conditions (i.e., with insufficiently masked or unmasked, clearly visible primes) than under NCE conditions (with effectively masked primes). Third, so far the only instance where repetition benefits rather than costs have been obtained in the masked prime task was an experiment where 90% of all trials required a response with the same hand, but again, priming effects of equal size were found for frequent (mostly repeating) and infrequent (mostly alternating) responses (Schlaghecken & Eimer, 2001).

Based on these observations, one might speculate that in the masked prime task, repetition costs reflect the participant's strategy to withhold any overt motor response (to the sudden onset of prime and/or mask) until the target has appeared. According to this view, the masked prime task represents a form of task-switching situation, with a 'withhold response' and an 'execute re-

sponse' task regularly alternating. Response repetition costs on task-switching trials are common, and have been interpreted as indicating, for example, a 'reconfiguration' of the cognitive system (e.g., Kleinsorge, 1999), or a response-suppression mechanism aimed a preventing accidental response repetitions (e.g., Hübner & Druey, in press). Such strategic processes are assumed to be mediated by frontal cortical areas (Band & van Boxtel, 1999; Faw, 2003). Consequently, according to the hypothesis that these areas mature during adolescence (Casey et al., 2001), age-related differences in repetition costs should be obtained, with the youngest children showing the largest costs, similar to findings of larger task switching costs (Cepeda, Kramer, & Gonzales de Sather, 2001; Reimers & Maylor, 2005) and larger flanker interference effects (e.g., Enns & Girgus, 1985; Ridderinkhof & van der Molen, 1995) in children compared to young adults.

INHIBITORY CONTROL IN CHILDREN AND YOUNG ADULTS

Based on these considerations, a dissociation between response repetition effects (repetition costs) and priming effects (NCE) was expected in the present experiment. The former was expected to show age-related differences, with larger effects – indicating less effective inhibitory control – for younger children. In contrast, the latter was expected to be largely unaffected by age. In particular, even younger children where expected to produce significant NCEs, suggesting that low-level self-inhibitory control is already operational at this age. Conversely, if self-inhibition processes were not yet sufficiently developed in younger children, then this group should show PCEs rather than NCEs (indicating prime-related response activation without subsequent self-inhibition).

Method

Participants

Sixty-four volunteers participated in the experiment. Fifty-seven of these (24 young children, 7-8 years, mean age 7.4 years, 13 males; 21 older children, 11-12 years, mean age 11.4 years, 10 males; 12 young adults, 16-23 years, mean age 20.2 years, 3 males) completed the task.[3] According to self-report or to parental-/teacher-report, all participants had normal or corrected--to-normal vision and no known history of neurological or behavioural disorders. Seven participants were left-handed according to self-/parent-/teacher-report. The children were drawn from two schools in Warwickshire, and written consent was obtained from parents or legal guardians via a response slip to a letter sent home from

the school. The letter contained a full debrief and highlighted the child's right to withdraw from the experiment at any time. Children were given a colourful sticker of their choice as a reward, regardless of whether or not they completed the experiment.

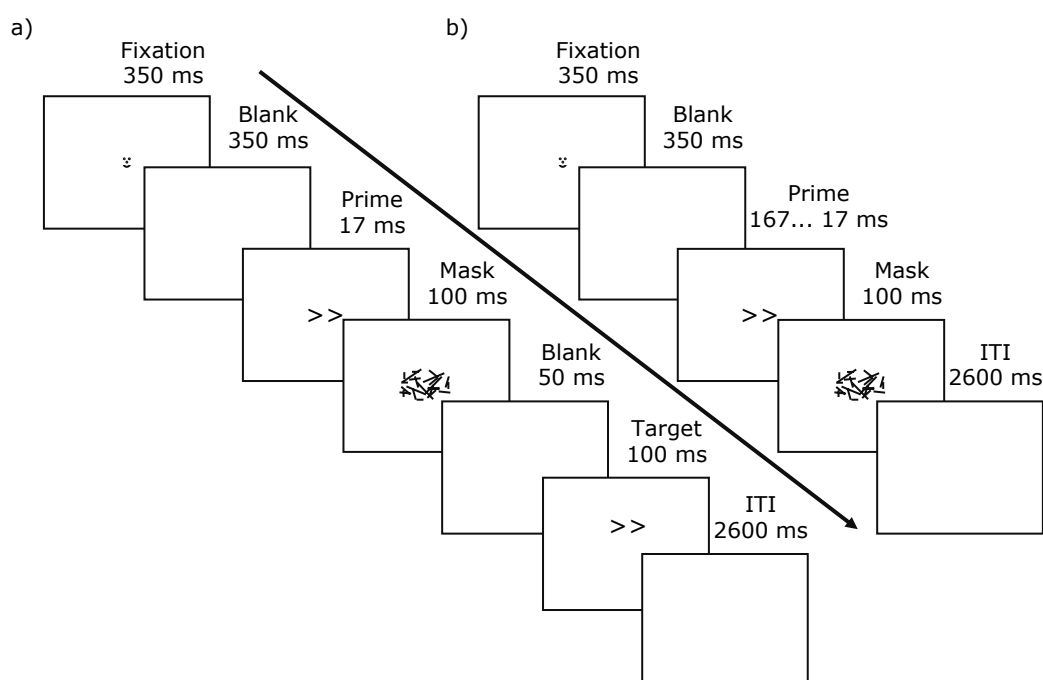### Stimuli and apparatus

Left-pointing and right-pointing double arrow heads ('<<' and '>>') served as primes and targets, and an outward-pointing double arrow ('<>') served as neutral prime. Primes and targets subtended a visual angle of approximately 1.2° x 0.4°. A small 'smiley face' (approximately 0.2° x 0.3°) served as fixation aid. Masking stimuli were constructed on the basis of a 6 x 5 matrix, randomly filled with overlapping horizontal, vertical, and oblique lines of different length (0.06° to 0.3°; width 0.06°), resulting in a roughly rectangular array of about 1.9° x 1.2°. On each trial, a new random mask was created in order to avoid perceptual learning of the mask, which could result in an increased ability to ignore the mask and a correspondingly increased ability to consciously perceive the prime (Schubö, Schlaghecken, & Meinecke, 2001).

Procedure

Participants were seated at a table in front of a laptop computer at a distance of 50 – 60 cm from the screen. They were instructed to maintain central eye fixation, and to respond with a left-hand key press to arrows pointing to the left, and with a right-hand key press to arrows pointing to the right. Response keys were the left and right SHIFT keys of the computer keyboard.

The experiment consisted of two parts. Part one was a masked prime RT task, consisting of 4 blocks of 48 trials each; part two was a prime identification task, consisting of 2 blocks of 40 trials each. Each part began with a brief (12 trials) practice block. Trial structure in each task is depicted in Figures 1a and 1b, respectively. Each trial began with the presentation of the central fixation stimulus for 350 ms, followed by a 350-ms blank screen, followed by a centrally presented and immediately masked prime. Mask duration was 100 ms.

In the masked prime RT task, primes were presented for 17 ms. Fifty ms after offset of the 100-ms mask, a target was presented for 100 ms, randomly and with equal probability either directly above or below fixation. Inter-Trial-Interval (ITI) was 2,600 ms. Trials were termed compatible when prime and target arrows pointed in the same direction, incompatible when they pointed in opposite directions, and neutral when the prime had no response assignment. Left and right target arrows, and compatible, incompatible, and neutral trials were equiprobable and randomised within

Figure 1

Experimental trial structure a) in the masked prime RT task (depicting a compatible trial, with prime and target arrow pointing in the same direction), and b) in the prime identification task.

each block. Participants were instructed to respond to the direction of the target arrows as quickly and as accurately as possible.

In the prime identification task, no target stimuli were presented after the mask. Prime duration was varied in a one-down/two-up staircase procedure such that on the first trial, prime duration was maximal (167 ms), and was on subsequent trials shortened in 17-ms steps (down to a minimum of 17 ms) whenever participants gave the correct response. Conversely, when participants made an incorrect response, prime duration on the next trial was prolonged by 33 ms. Participants had to respond to the direction of the masked prime arrow, and were instructed to "just guess" on trials where they did not consciously perceive the prime arrow. They were informed about the staircase procedure, and were told that during this part, only response accuracy, but not response speed, was of relevance. ITI was again 2,600 ms.
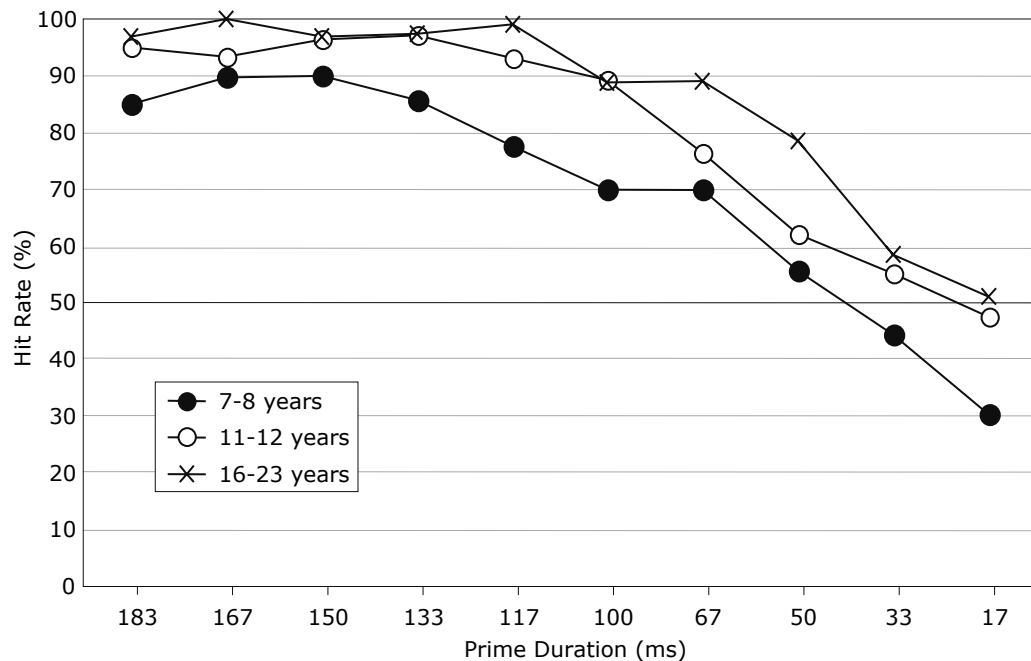
Results

Twelve participants had problems with the demands of the masked prime RT task (producing overall error rates of more than 15% and/or failing to give a response on more than 10% of all trials and/or pro-

ducing RTs of more than 2 standard deviations above the group mean). After confirming that neither mean RTs nor mean error rates correlated with the effects of masked primes on RTs (i.e., incompatible RT minus compatible RT; both rs < 0.2, both ps > .57), these participants were excluded from analysis, leaving 18 participants in the 7-8 group, 16 participants in the 11-12 group, and 11 participants in the 16-23 group. No further data trimming procedure was employed. For the subsequent analyses, a significance level of .05 was chosen. Greenhouse-Geisser adjustments to the degrees of freedom were performed where appropriate (indicated in the results section by ε), and corrected p-values are reported.

Prime identification task

After discarding the first 10 trials of each staircase block as 'warm-up' trials, mean prime duration in the prime identification task was calculated. A one-way analysis of variance (ANOVA) was computed on this value for the variable Age. Mean prime duration decreased with age from 86.5 ms (SD = 21.1) to 63.5 ms (19.3) to 51.6 ms (13.8) for the 7-8, 11-12, and 16-23 year olds, respectively, $F(2, 42) = 12.96$, $p < .001$. A repeated measures ANOVA was com-

Figure 2

Percent correct responses in the Prime Identification task, plotted separately for each prime duration and age group (7-8 year olds black circles; 11-12 year olds: white circles; 16-23 year olds: cross marks).

puted on the percentage correct responses for the variables Prime Duration (167, 150, 133, 117, 100, 83, 67, 50, 33, and 17 ms) and Age (7-8, 11-12, 16-23). As can be seen from Figure 2, percentage of correctly identified primes decreased drastically with decreasing prime duration, $F(9, 378) = 75.92$, $p < .001$, $\varepsilon = .593$, and was generally higher in adults and older children than in younger children, $F(2, 42) = 13.85$, $p < .001$. However, these factors did not interact, $F(18, 378) = 1.29$, $p = .23$, $\beta = .32$. Subsequent one-sample t-tests compared percentage correct responses for each prime duration with chance level accuracy (50%), separately for each age group. For the 7-8 year olds, percentage correct was significantly above chance level only for prime durations of 67 ms and more, with all ts > 4.1, all ps < .002, whereas for 10-11 year olds and 16-23 year olds, it was significantly above chance level for all prime durations of 50 ms and more, all ts > 3.2, all ps < .007.

Masked prime RT task

For compatible, neutral, and incompatible trials in the masked prime RT task, ANOVAs were computed on mean correct RTs and on error rates for the variables

Compatibility (compatible, neutral, incompatible) and Age. Performance data (RTs and error rates) on each trial type and priming effects are presented in Table 1. Error rates were somewhat higher in the 7-8 year olds than in the other two groups, $F(2, 42) = 4.66$, $p = .015$. There were no other effects on error rates (main effect of compatibility, and Age x Compatibility interaction: both Fs < 1, both ps > .5, both βs > .8). It should be noted, though, that there was at least a numerical NCE (fewer errors for incompatible than for compatible trials) for each age group, indicating that the NCE on RTs does not reflect a speed/accuracy trade-off. However, this effect was significant only for the oldest group, $t(10) = 2.17$, $p = .028$, one-tailed, both other ts < 1, both ps > .4.

Overall RTs decreased with increasing age, $F(2, 42) = 22.39$, $p < .001$, and were longer on compatible and neutral trials than on incompatible trials, $F(2, 84) = 6.39$, $p = .004$, $\varepsilon = .913$. Importantly, these effects did not significantly interact, $F < 1$, $\beta = .94$. In fact, subsequent one-tailed paired t-tests confirmed that RTs were significantly longer on compatible than on incompatible trials in each group: $t(17) = 2.04$, $p = .029$, $t(15) = 2.36$, $p = .016$, and $t(10) = 3.29$, $p = .004$, for the 7-8 year olds, the 11-12 year olds, and the 16-23 year olds, respectively.

Table 1

Mean reaction time (RT) and error rate for compatible, neutral, and incompatible trials in the masked prime blocks, together with priming effects (incompatible minus compatible), separately for each age group, with standard deviation in parentheses.

Age Group (years)	Measure	Compatible	Neutral	Incompatible	Priming	
7-8	RT (ms)	628 (116)	628 (121)	618 (110)	-10*	(21)
	Error Rate (%)	4.9 (4.2)	5.2 (4.0)	4.8 (4.3)	-0.1	(3.4)
11-12	RT (ms)	506 (54)	502 (57)	496 (60)	-11*	(18)
	Error Rate (%)	2.3 (3.6)	1.7 (2.4)	2.2 (1.9)	-0.2	(3.1)
16-23	RT (ms)	417 (56)	417 (59)	405 (64)	-12**	(12)
	Error Rate (%)	3.4 (3.4)	2.6 (3.1)	2.1 (2.0)	-1.3*	(2.0)

 * $p < .05$, one-tailed

** $p < .001$, one-tailed

Table 2

Mean reaction time (RT, in ms) for response alternation trials ('alternate') and response repetition trials ('repeat'), together with repetition effects (repeat minus alternate), separately for each age group, with standard deviations in parentheses.

Age Group	Alternate	Repeat	Difference	
7-8	596 (103)	660 (125)	64**	(51)
11-12	488 (61)	515 (54)	27**	(20)
16-23	405 (58)	421 (63)	16*	(17)

 * $p < .05$

** $p < .001$

To account for the general RT decrease with increasing age, follow-up analyses were conducted on scaled priming effects, calculated by dividing RT on compatible trials by RT on incompatible trials for each participant separately. These analyses confirmed that each group produced significant NCEs (indicated by a scaled value larger than 1), $t(17) = 2.02$, $p = .030$, $t(15) = 2.52$, $p = .012$, and $t(10) = 3.19$, $p = .005$, for the 7-8 year olds, the 11-12 year olds, and the 16-23 year olds, respectively. Again, the size of these effects did not differ significantly between groups, $F < 1$, $\beta = .81$.

Response repetition effects

Mean RTs on response repetition trials (trials requiring the same response as the immediately preceding trial) were compared with mean RTs on response alternation trials (trials requiring a different response than the immediately preceding trial). In either case, only trials where both the current response and the preceding response were correct were taken into account. Mean RTs on each trial type and repetition effects are presented in Table 2. Responses were generally slower on repetition trials than on alternation trials, $F(1, 42) = 43.22$, $p < .001$. Importantly, this effect interacted with age, $F(2, 42) = 7.66$, $p = .001$, being largest for the 7-8 year olds, intermediate for the 11-12 year olds, and smallest for the 16-23 year olds. Again, the same pattern was observed when effect size was scaled (by calculating repetition costs as RT on repetition trials divided by RT on alternation tri-

als for each participant separately): Younger children still showed the largest, and young adults still showed the smallest repetition costs, $F(2, 42) = 4.83$, $p = .013$.

DISCUSSION

The present study investigated masked motor priming effects in young (7-8 years) and older (11-12 years) children and in young adults. Results were fully in line with the predictions: Prime identification performance indicated that participants were not able to reliably identify masked primes presented for 17 or 33 ms, suggesting that the 17-ms masked primes employed in the RT task were subliminal. In the masked prime RT task, younger children produced, unsurprisingly, substantially longer RTs than older children, who in turn produced longer RTs than young adults. Nevertheless, as expected, all three groups showed significant priming effects in the form of NCEs. The size of the NCE did not show any statistical difference between age groups. In contrast, response repetition effects showed a significant decrease with increasing age.

Summary: Low-level and high-level inhibitory control

Obviously, it is not possible to base any firm conclusion on a failure to reject the null hypothesis: Not finding a significant difference in NCEs between age groups

does not prove that there is none. Furthermore, the high *β*-value for the relevant interaction (i.e., the low observed power) indicates that it might be extremely difficult to ever find a statistically significant difference, even if it existed. Therefore, it is not possible to directly draw the conclusion that children and young adults produce the same masked priming effects.

Low-level control: The NCE

However, in line with the hypothesis, the data clearly show that children do produce significant NCEs. This finding stands in marked contrast to results from a study investigating masked priming effects in old age (Schlaghecken & Maylor, 2005), where older participants (mean age: 75.6 years) showed substantial priming effects in the form of PCEs when targets followed the masked primes immediately, but failed to produce reliable NCEs when target onset was delayed. In the present context, the relevant aspect of this finding is that it is consistent with the assumption that the NCE reflects self-inhibition and disinhibition processes mediated by the basal ganglia, as this structure – in particular the neostriatum – shows substantial age-related volume loss (e.g., Raz, 2001).

Furthermore, it is interesting to note that the present results are reminiscent of the finding that young children only show impaired performance when responding to a target at a previously attended location (IOR) when their attention has been exogenously removed from this location in the double-cue paradigm. In contrast, they fail to show IOR when they have to shift attention endogenously in a single-cue paradigm (MacPherson et al., 2003). The authors have interpreted this finding as indicating that in the single-cue paradigm, attention first has do be disengaged voluntarily from a spatial location before the automatic process of IOR can become active. The voluntary disengagement of attention is thought to be mediated by anterior cortical areas that are immature in children. Consequently, they do not show IOR in the single-cue paradigm. The IOR process itself, however, is assumed to be mediated by subcortical structures that are already well developed in early childhood. Therefore, IOR can be observed in young children in the double-cue paradigm, where attention is exogenously (involuntarily) removed. The same argument can be applied to the present results: Whereas repetition effects reflect strategic processes mediated by late maturing frontal cortical areas, the NCE reflects a low-level, automatic self-inhibition process, which prevents activation of a response that is no longer supported

by perceptual information and is mediated by early maturing subcortical structures.

High-level control: Response repetition costs

High-level or strategic processes are generally assumed to be a function of executive control processes mediated by anterior – specifically prefrontal – cortical areas (e.g., Band & van Boxtel, 1999; Dempster, 1992; Faw, 2003; Harnishfeger & Bjorklund, 1994; Spence & Frith, 1999). Because maturation of the frontal cortex continues well into adolescence (Casey et al., 2001), it is not surprising to find that voluntary control continues to improve even during adolescence (e.g., Brocki & Bohlin, 2004; Leon-Carrion et al., 2004). For example, larger interference effects in children compared to adolescents and young adults have been observed in response conflict paradigms such as the flanker task (e.g., Enns & Girgus, 1985; Ridderinkhof & van der Molen, 1995), indicating immature (i.e., less efficient) inhibitory control and/or stronger susceptibility to interference in younger children due to their immature frontal lobes (for an overview, see van der Molen, 2000).

Of particular interest in the present context is the finding that children also show larger switch costs in the task-switching paradigm than young adults (Cepeda et al., 2001; Reimers & Maylor, 2005). In line with the above interpretation, this can be regarded as reflecting children's less efficient top-down control. Task switching situations appear to selectively impair response repetition: Whereas in most situations repetition benefits are observed, with shorter RTs when the response is the same as on the preceding trial, the reverse pattern has been observed on task switching trials. Although different interpretations of this effect have been put forward (e.g., Hübner & Druey, in press; Kleinsorge, 1999; Schuch & Koch, 2004), it seems to be generally agreed that the same top-down control process that enables successful task switching also interferes with the execution of a repeated response. If this is the case, then one might speculate that the more efficient (fast, targeted) the top-down control process, the less it interferes with response execution. In other words, both repetition and switch costs should be larger in individuals with inefficient top-down control than in individuals with efficient top-down control.[4] Accordingly, young children should show not only increased switch costs, but also increased repetition costs.

Obviously, the masked prime task does not employ a task-switching paradigm in the strict sense. However, at a very general level, some similarities exist. In the masked prime paradigm, each trial begins with a prime stimulus followed immediately by a mask. Compared to prime and target arrows, the masking stimulus is per-

ceptually very salient. It therefore might trigger a premature response if participants do not adopt an overall strategy to withhold responses until target presentation. Therefore, the masked prime paradigm might be seen as a specific form of a task-switching paradigm, where participants have to regularly alter between a nogo task (in response to the mask and/or prime) and a go task (in response to the target). The present finding of repetition costs in the masked prime task might therefore be interpreted as reflecting interference from top-down inhibitory control processes, in analogy to the interpretation of task-switching repetition costs. Correspondingly, the finding of larger repetition costs in children than in young adults is consistent with the notion of young children's less efficient control and stronger susceptibility to interference, due to their immature frontal lobes.

'Emergency brake' and alternative interpretations of the NCE

Withholding a response to a clearly visible but – as per instruction – response-irrelevant stimulus requires voluntary, high-level inhibitory control mechanisms. In contrast, it seems likely that suppressing a response tendency triggered by a subliminal prime involves processes generated at low-level and automatic stages of the visuomotor system. As outlined above, we assume that the prime triggers an activation of its corresponding motor response, and that a self-inhibition process actively suppresses this initial response tendency when it is suddenly no longer supported by sensory evidence (Eimer & Schlaghecken, 2003; Schlaghecken & Eimer, 2002). However, alternative interpretations of the NCE have been put forward recently (Lleras & Enns, 2004; Verleger, Jaśkowski, Aydemir, van der Lubbe, & Groen, 2004). According to these accounts, the NCE does not reflect self-inhibition of the initially primed response, but simply activation of the opposite response triggered by task-relevant features contained in the mask.

With respect to this alternative interpretation, it is of particular interest to note that the NCE – but not the preceding PCE with short mask-target SOA – is reduced or even absent in older adults (Schlaghecken & Maylor, 2005; Seiss & Praamstra, 2004), indicating that ageing selectively affects low-level self-inhibition and/or disinhibition processes, but leaves low-level activation processes unaltered. In contrast, the 'activate-the-opposite' hypothesis can not account for the selective age-related changes in NCE: If response activation processes are affected by age, then similar age-related changes should have been obtained for the PCE with the short SOA. This was not the case. Conversely, if low-level activation processes are

not affected by age – as evidenced by the normal PCE in older participants – then, according to the 'activate-the-opposite' assumption, the NCE should also not have been affected. Furthermore, the mask-induced activation hypothesis fails to account for the finding that NCEs have been observed with masks that do not contain any potentially task relevant features (Klapp, 2005; Schlaghecken & Eimer, 2004a). Therefore, it seems reasonable to assume that the NCE does in fact reflect low-level self-inhibition of the primed response (and corresponding disinhibition of the alternative response) rather than mask-induced low-level activation of the opposite response.

This type of inhibition appears to be fundamentally different from voluntary, high-level inhibitory control, which requires conscious awareness of the task-relevant stimuli and is mediated by anterior cortical areas. A recent fMRI study with young, healthy adults (Aron et al., 2003) found self-inhibition and disinhibition in the masked prime task to be associated with signal changes in the thalamus and the basal ganglia. Activation was also observed in the posterior parietal cortex, but not in the prefrontal cortex or in other anterior areas (Eimer & Schlaghecken, 2003). This finding stands in marked contrast to the prefrontal activation usually obtained in studies of (voluntary) response inhibition in stop-signal or go/nogo tasks (e.g., Konishi et al., 1998; Menon et al., 2001). However, the result is consistent with the notion that whereas anterior brain areas mediate voluntary control processes, unconscious processing and automatic motor control are a function of posterior parietal (Pisella et al., 2000) and subcortical (e.g., Heyder, Suchan, & Daum, 2004; Kelly et al., 2004) circuits. In line with this, evidence has been obtained that self-inhibition (as evidenced by the NCE) is unaffected by repetitive transcranial magnetic stimulation of anterior (motor and premotor) structures (Schlaghecken et al., 2003), but is substantially altered in patients with basal ganglia-related movement disorders (Aron et al., 2003; Seiss & Praamstra, 2004). Together with the present findings, these results provide converging evidence that self-inhibition in the masked prime task can be regarded as a low-level, automatic control process, which is mediated largely by subcortical structures and does not involve central executive processes in anterior cortical areas.

Automatic control and the role of intentions

The pattern of results from the present experiment is consistent with the notion that automatic processes develop earlier than controlled processes (for a review, see Plude, Enns, & Brodeur 1994). The self-in-

hibition process underlying NCEs in masked priming is assumed to act as an 'emergency brake' process, capable of counteracting the perceptuo-motor system's ability to respond to even the most fleeting of sensory stimuli. Such stimuli can quickly activate a corresponding motor response, even if they have not (yet) been consciously perceived. Clearly, such a 'direct' response mode (Neumann & Klotz, 1994) is advantageous for an organism that has to adjust its ongoing behaviour on-line in a constantly changing and potentially hostile environment. There are, however, obvious disadvantages as well: If all potentially task-relevant stimuli, no matter how irrelevant they are at the time, would automatically elicit a motor response, then coherent behaviour would not be possible. Thus the ability to quickly initiate a response is only useful if accompanied by the ability to quickly suppress the response if it turns out to be inappropriate.

In the case of consciously perceived, supraliminal stimuli, full information about all stimulus attributes is available, so that the decision of whether or not a pre-activated response needs to be inhibited can be made in a controlled and, hence, flexible and task-appropriate way. This ability improves during childhood and adolescence, as evidenced here by the decrease of repetition costs with increasing age. With subliminal stimuli, in contrast, such controlled decisions are not possible, and a more automatic system needs to be in place. We have argued elsewhere (Schlaghecken & Eimer, 2002) that a subliminally triggered motor activation will be inhibited whenever (1) it is relatively strong and, thus, has the potential to affect overt behaviour, but (2) the perceptual evidence for this activation has suddenly disappeared (as in the case of successful backward masking).

Interestingly, though, it appears that these automatic control processes are not independent of current intentions. In several studies, it has been demonstrated that the impact of subliminally presented primes on behavior is mediated by the currently active task set. If primes do not match the set of stimulus-response (S-R) mappings imposed by the task instructions, and applied by the participant, then they will cease to exert any influence on overt motor responses (e.g., Ansorge, Heumann, & Scharlau, 2002; Eimer & Schlaghecken, 1998; Klapp & Haas, 2005; Klapp & Hinkley, 2002; Kunde, Kiesel, & Hoffmann, 2003; Neumann & Klotz, 1994; Schlaghecken & Eimer, 2004b). Thus while subliminal stimuli might trigger processes that are clearly low-level and automatic (outside voluntary control), these processes nevertheless depend on high-level intentional states. Presumably, the intention to

respond, for example, with a left finger movement to an arrow pointing to the left and with a right finger movement to an arrow pointing to the right results in a specific 'configuration' of the perceptuo-motor system, which makes it particulary susceptible to certain inputs (i.e., left- and right-pointing arrows) and particularly likely to execute certain responses (left and right finger movements). However, once this intention has been implemented (i.e., once the perceptuo-motor system has been configured in the required way), low--level control processes can occur without higher-level or voluntary 'supervision,' such that if a strong initial activation is suddenly no longer supported by sensory evidence, it will automatically self-inhibit.

We have demonstrated that such a system will only require local self-inhibition circuits, without the need for top-down inhibitory executive control mechanisms (Bowman et al., in press). Self-inhibition is a basic functional principle in cognitive control and a common mechanism in the nervous system (Arbuthnott, 1995). Because of its relative simplicity, it seems reasonable to assume that this mechanism is one of the earliest to develop both phylogenetically and ontogenetically (although we are not aware of any studies investigating this issue yet). If this assumption is correct, then it should be possible to observe comparable NCEs not only in adults and children, but also in non-human animals. Such studies could help to shed more light on the function of fundamental, low-level control processes that allow an organism to adjust its ongoing behaviour quickly and flexibly to rapid changes in its enviroment.

Notes

[1] It should be noted that this is not supposed to imply a specific view on the mechanisms underlying visual backward masking. It is of no concern in the present context whether masking entails interruption (e.g., Turvey, 1973), interactions between spatial frequency channels (e.g., Breitmeyer & Ganz, 1976; Delord, 1998), or object substitution (e.g., Enns & Di Lollo, 2000). The

relevant issue is that because of the mask, the motor system is deprived of the unique, unequivocal evidence for one particular response.

[2] Alternative interpretations of the NCE which do not assume the existence of inhibitory control processes will be considered in the General Discussion.

[3] For various reasons, seven children did not success-fully complete the experiment: some walked out before the end of the experiment, some took short breaks during an experimental block, others completed the experiment but then admitted that they had not really been able to see the stimuli because they had forgotten their glasses, etc.

[4] Unfortunately, we are not aware of any studies in-vestigating the correlation between switch costs and repetition costs, which would allow us to test this hy-pothesis directly.

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