

an alternative action for the subsequent trial in order to regain complete reward. This supports the view that pFMC signals the need for adjustments required for goal achievement.

Extending this view, findings in non-human primates and human neuroimaging studies demonstrate that unexpected occurrence of negative feedback activates the same region in pFMC as response errors [4,5]. Moreover, neuroimaging studies on response conflict and decision uncertainty also showed activity in the pFMC [6].

How can this view be reconciled with the finding of pFMC activity during social exclusion [1,7]? As Williams and colleagues recently showed, participants who are excluded from a game make attempts to be re-included, such as search for eye contact and gestures ([8] and pers. commun., *Tagung der Fachgruppe Sozialpsychologie IX*). In the scanner, such attempts to be re-included in the game are restricted to futile button presses and vocal responses. Although these actions seem unpromising, it is conceivable that participants implemented such remedial actions also in the fMRI study by Eisenberger *et al.* As the investigation of these attempts seemed not to be the primary focus of the study on social exclusion, no information on this aspect is provided [1,7].

Neuroimaging and patient studies implicate the pMFC also in autonomic responses [9]. These autonomic responses support the affective, distressing aspects of events signaled by the pFMC. Importantly, they also provide the appropriate somatic state for behavioral changes. To summarize, we suggest that the pFMC monitors potential and real divergence from the intended and expected state of the individual, and signals the need for behavioral changes to prevent harm and to optimize goal achievement. This signal seems to be conveyed to regions involved in cognitive and motor control, autonomic and affective regulation, rendering it an essential

prerequisite of flexible, adaptive human behavior. It needs to function on all levels of information processing, starting with primary reinforcers (reward, pain), including increasingly abstract cognitive operations (monitoring for errors, response conflicts and uncertainty), and extending even to the social level. We wish to underline that even very complex behavioral phenomena can be reconciled with basic cognitive principles of reward processing and adaptive behavior.

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doi:10.1016/j.tics.2004.08.013

Letters Response

The neural alarm system: behavior and beyond. Reply to Ullsperger *et al.*

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In a recent review, we suggested that the dorsal anterior cingulate cortex (dACC) could be thought of as a component in a ‘neural alarm system’ [1]. Ullsperger, Volz and von Cramon have responded by suggesting that the purpose of this alarm is signaling the need for behavioral change [2]. In their words, ‘an alarm signal makes sense only when it is used for subsequent actions

leading to desired consequences.’ They go on to suggest that the dACC activity observed during social exclusion [3] may be a consequence of button presses and vocalizations on the part of participants trying to be re-included, akin to what might occur in a face-to-face analogue of the experiment.

In responding to Ullsperger, Volz and von Cramon we want to acknowledge that we largely agree with their claim. We would go so far as to suggest that behavioral

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change or planning might be the modal consequence of dACC activity. However, we do not believe that behavioral change is the only consequence of dACC activity. There is likely to be a wide array of consequences that include behavior, cognition, affect, and peripheral nervous system activity. Although some cognition and affect might serve to mediate the relationship between dACC and behavioral change, this is not always the case. In humans, unlike other animals, an alarm signal can set in motion contemplation and introspection, not for the purpose of an immediate response but simply to understand the nature of one's social environment or to consider how the event producing the alarm reflects on one's identity and self-worth. Other work of ours (as yet unpublished) suggests that for those who score highly in dispositional self-consciousness, dACC responses to conflict lead to medial prefrontal activations associated with introspection rather than the typical lateral prefrontal regions associated with response planning. Such mental activities might have behavioral consequences in the days or weeks that follow, but it is not obvious that this is the goal of such introspective processes.

Kip Williams has indicated (pers. commun.) that in all the Cyberball sessions he has personally observed, he has never seen excluded participants engage in button presses or vocalization. In our study [3], we did not measure button presses, but we did find that the region of motor cortex associated with finger movements was more active during the inclusion than the exclusion condition and was not active in the exclusion condition relative to rest. These results suggest that the dACC activity observed in our study cannot easily be attributed to behavioral activity during exclusion.

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doi:10.1016/j.tics.2004.08.014

Letters

The mental number line: exact and approximate

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Reviewing behavioral and neural data in children, humans and animals, Feigenson *et al.* [1] distinguish two core systems for number representation. One system represents number in an exact way but has a fixed upper limit; the other system has no size limit but represents number only approximately. Both systems are claimed to have a phylogenetic origin and to constitute the basis for ontogenetic development. As such, each system's representational principles are reflected in adult human performance: subitizing is ascribed to the exact system whereas symbolic number processing is based on a mapping to the approximate system. This last assumption is motivated by the robust finding that symbolic numbers are more difficult to discriminate with increasing size (the 'size effect'). However, it remains to be shown how this mapping can reconcile the inherently exact nature of a symbolic system with signatures of approximate processing such as the size effect.

Recent behavioral evidence and computational modeling from our laboratory speak directly to some of the issues raised by Feigenson *et al.* First, we have shown that an approximate number line with the same properties as

observed with monkey single-cell recording [2] can arise in uncommitted neurons under unsupervised learning conditions [3]. This finding challenges the assumption of a phylogenetically determined number line.

Second, we formulate a concrete proposal of how symbolic number performance builds on this early available approximate number line. Remarkably, the same number line that represents non-symbolical number approximately comes to represent symbolic number exactly. In a follow-up study we showed how this linearly scaled number line explains the size effect [4]. The crucial factor is that the negative correlation between frequency of occurrence and number size [5] necessarily leads to non-linear mappings from number line to a binary decision mechanism (smaller/larger). The explanatory power of this idea exceeds that of approximate representations [6,7] because it accounts for behavioral signatures of linearity of the number line that were not addressed by Feigenson *et al.* – symmetry in distance-related priming [8] and absence of a size effect in tasks other than numerical comparison that also show number line involvement [4]. This exact representation is restricted to small numbers, depending on frequency of exposure but, at least in adults, certainly beyond single digit numbers.

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