with suggestions that concern the function of the nor-adrenergic neurones of the locus coeruleus[40]. Dopaminergic neurones and noradrenergic neurones show strikingly similar responses to salient events (for reviews see Refs 8,40), both having a slow spontaneous rate of discharge (1–8 spikes/s) that is interrupted by a short-latency (~50–100 ms), short-duration (~100 ms) burst of pulses in response to unexpected novel stimuli (of all modalities), or to primary reinforcers. In both classes of neurone the reaction to such stimuli involves a significant proportion of the cell population, while neither class responds reliably to consummatory movements or to stimuli in highly automatized tasks. Furthermore, in both classes, repeated non-reinforced presentation of a neutral stimulus leads to response habituation, which can be reinstated by association with primary reward. In summary, both dopaminergic and noradrenergic neurones are maximally activated by unexpected stimuli that are made salient by virtue of their novelty, their status as primary reinforcers or their association with primary reinforcers. In the case of noradrenergic neurones, it has been argued by Aston-Jones and his colleagues[40] that this response profile is indicative of a functional system that is primarily involved in the regulation of attention to the external environment and readiness to respond to unexpected events. Our current proposal is that the short-latency dopamine response performs a similar function within the basal ganglia. If the supposition that selection is a core function of the basal ganglia is correct[16,17], this dopamine response could assist in preparing the animal to deal with the unexpected by promoting the switching of attentional and behavioural resources towards biologically significant stimuli.

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LETTERS TO THE EDITOR

From grasping to speech: imitation might provide a missing link

Rizzolatti and Arbib[1] present an intriguing theory on the evolution of a neural substrate that promotes language abilities in humans. In an impressive series of papers Rizzolatti and his co-workers[2] have revealed a distinct neural system in the premotor area of the monkey brain that 'matches observed events to similar, internally generated actions'[1]. They argue that this system is capable of recognizing the motor actions of another individual and uses the resultant information to execute similar actions. Furthermore, they suggest that this neural representation might be accessible to other neural systems involved in imitation.

In my view their proposal has the following key features: (1) a conspecific's motor behaviour presents a biologically meaningful visual input; (2) the system is able to map this visual input onto motor neurones, while it is expressing generalization and categorization properties; (3) the same motor system is able to execute the same or a similar action; and (4) the actual execution is, however, under inhibition but could be released in special situations.

Without debating the relevance of this theory to human language, I would like to stress another important aspect of this theory that relates to our understanding of imitative behaviour in the animal kingdom. The ability of animals to imitate received a renewed interest in recent years[3–5]. In general, imitation means that the observer copies 'some aspect(s) of the intrinsic form of an act'[3]. As a result of recent discussions, levels of increasing complexity are applied to categorize instances of animal imitation: (1) copying increases the frequency of an already acquired motor pattern or changes its orientation in space ('response facilitation')[4]; (2) copying modifies the motor pattern of an already acquired action ('action-level imitation')[4]; and (3) copying changes the sequential relations between actions ('sequence imitation')[5].

However, definite neural mechanisms for these abilities have not yet been identified.

Many authors argue that imitation can only be performed by forming cross-modal associations, which requires complex neural computing, as, for example, the visual perspective of the actor and of the observer is usually different[6]. It is often argued that the need for complex representational capacities on the part of the observer present a limit to most animal species.

I would suggest that the observation–execution matching system (OEMS) described by Rizzolatti and Arbib[1] might provide us with a general theory that explains imitative phenomena and that also places these abilities in an evolutionary context. Accordingly, the following parallel or sequential steps that lead to the development of OEMS can be suggested: (1) animals are able to recognize species-specific motor patterns in conspecifics, for example, submissive signals, bird song; (2) they are prepared to execute either complementary (for example, submissive behaviour pattern to a dominant signal) or concordant (for example, many aggressive displays) species-specific motor patterns; (3) in a learning situation, animals could recognize the species-specific behaviour of their companion and execute a similar motor pattern on the basis of OEMS; and (4) in more complex cases, where pre-existing species-specific motor patterns should be modified by observation, OEMS would facilitate categorization of the perceived action and the observer could devote more time to observing and learning the peculiarities of the motor pattern. The observation–execution matching system could also support a secondary representation of these imitated actions with reference to the underlying species-specific movement. These features of OEMS confer even more of an advantage to species with a broad range of freedom of movements by facilitating the pre-categorization of observed actions.

From the evolutionary point of view it should be explained, however, why monkeys do not seem to be able to imitate (contrary to the widely held belief), whereas apes do (and neither species possesses natural language abilities). Additionally, many instances of imitation in birds have been described recently[7,8], which suggests a convergent parallel evolutionary path for the same phenomenon. One could argue, from the functional (ultimate) point of view, that the ability to copy the motor pattern of a conspecific (re-)emerges only in species where it has adaptive value. The value of OEMS theory is that it offers a testable hypothesis for the comparative analysis of imitation in animals that live in different ecological and social environments.

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Reply

We are grateful to Miklósi for his interesting remarks on our article[1]. We fully agree with him that the observation–execution mechanism we discovered in the monkey premotor area F5 is by no means unique to primates. We also believe, as he does, that the F5 'mirror' mechanism represents a particular variant of an ancient mechanism that underlies a variety of behaviors. In our own laboratories, we are exploring different issues, including imitation (see below), in which an observation–execution system is most probably involved. Considering the various levels of complexity of the motor system our view is that there are at least two radically different types of mirror phenomena. The first is one in which an executive sector of the motor system 'resonates' during the observation of an action. As a consequence the observed action is usually emitted. In this type of resonance phenomenon the understanding of the meaning is neither essential nor required. Examples of this 'resonance behavior' are some release phenomena in birds (see Ref. 2) and more generally those phenomena that Byrne describes under the term of 'response facilitation'[3]. The second concerns the motor areas of higher order in which action plans are coded. In this case the internal copy of the observed action is typically not repeated but used as the basis for understanding the actions made by the acting individual. Understanding could, of course, also lead to imitation of the observed action although, as distinct from the first type of resonance phenomena, the individual here will not repeat the movements he has seen obligatorily, but will be interested only in achieving the goal of the action. 'Echopraxia' and 'imitation behavior' are two pathological examples that reveal these two different resonance mechanisms[4]. The question of which actions a monkey understands and is able to repeat is very interesting. Unfortunately, so far, ethologically meaningful stimuli have been used in only a few neurophysiological studies (for examples see Refs 5–7). Thus, many of the important questions that Miklósi raises in his letter have currently no empirical answer, although they certainly deserve increased attention.

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Letters to the Editor

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