stimulus. Rich opportunities exist for further exploration of correspondences between behaviour, TMS and other physiological measures.

Little is known at the single-neuron level about the mechanisms mediating TMS effects. One recent study by Klaus Funke and colleagues reported that a single high-intensity TMS pulse applied to V1 neurons produced a temporal sequence of initial suppression of neuronal excitability, lasting about 100–200 milliseconds, followed by a period of rebound excitation. Understanding how such long suppression effects may cause interactions between TMS pulses delivered in trains will be an important step in clarifying the effects of repetitive-pulse TMS.

A final area of technical combination is that of using TMS in pharmacological studies. Following a demonstration that rTMS of motor cortex induces the release of dopamine in the putamen, Strafella and colleagues delivered rTMS to the motor cortex of subjects in the early stages of Parkinson's Disease (PD) and measured subsequent changes in dopamine concentration. In the patients' symptomatic hemisphere, the TMS-induced dopamine release was less than in the asymptomatic hemisphere but the area over which it was released was greater, suggesting a loss of specificity in corticostriatal communication in early PD.

Conclusions
In this Primer we have been able to give only a snapshot of the basic features and the applications of TMS. Some fundamentals of the use of TMS are falling into place as we learn more about the effects of different combinations of stimulus intensity, frequency, task and behavioural state. We have not had space to cover some important areas, such as studies of depression, language, eye movements and basic motor physiology, but the technique is now used in almost every

area of cognitive neuroscience. Areas in which we can expect the next major advances in the use of TMS (and TDCS) include: the combination of TMS with other techniques to investigate causal interactions between cortical areas; the development of new paradigms to change selectively the baseline state of cortical excitation prior to further magnetic stimulation; and the incorporation of TMS into neuro-rehabilitation programmes.

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Asymmetric tail-wagging responses by dogs to different emotive stimuli

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Research on behavioural asymmetries associated with specialisation of the left and right side of the brain has focused on asymmetric use of paired organs, such as forelimbs [1]. However, control of medial organs such as the tail would also be expected to involve hemispheric collaboration and, sometimes, competition. Here we report some unexpected and striking asymmetries in the control of tail movements by dogs: differential amplitudes of tail wagging to the left or to the right side associated with the type of visual stimulus the animals were looking at.

Thirty dogs, 15 intact males, 15 intact non-oestrus females, of mixed breed, with an age range of 1–6 years were tested. All were family pets whose owners had consented to participate in the experiment during periodic obedience and agility training in a behavioural dog school associated with the Faculty of Veterinary Medicine of Bari University, Italy.

The dogs were tested in a large rectangular wooden box (250 cm x 400 cm x 200 cm) uniformly covered inside with black plastic that prevented dogs from seeing outside. Illumination in the box was provided by four light bulbs (60 W) symmetrically located around the walls. The testing box had a rectangular opening (120 cm x 60 cm; 10 cm above the floor level) on the centre of one of its shorter side to permit the presentation of the stimuli. An opaque plastic panel, same size as the rectangular opening,
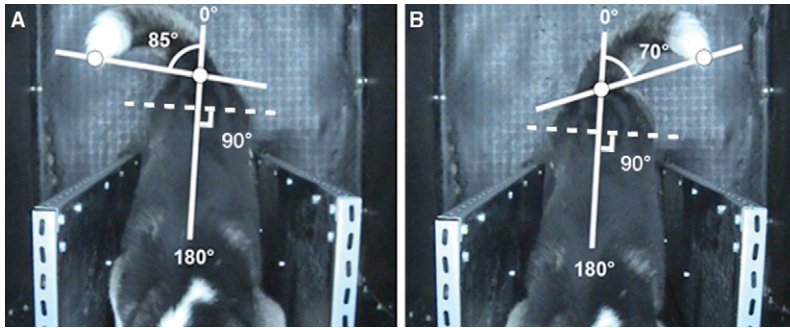
Figure 1. Methods to estimate angles to score amplitude of wagging behaviour of the dogs.
Angle A: wagging to the right; angle B: wagging to the left.

could be removed from the opening to allow sight of the stimuli. A superimposed metal grid prevented dogs from coming out through the opening. Two metal panels covered with black plastic (150 cm high, 60 cm in depth) were located on the two sides of the rectangular opening, to favour a centred position of the dog with respect to the video recording area during the experiment (Figure 1). A white panel was located behind the test stimulus to prevent vision of any other distracting stimulus.

In each trial the dog was introduced singly into the testing box and the stimulus was presented for 60 seconds. After an inter-trial interval of 90 seconds another stimulus was shown. The stimuli used were: the dog's owner; an unknown person; a dominant unfamiliar dog; and a cat.

We also tested dogs in the absence of any specific visual stimulus: the opaque plastic panel was removed from the opening for 60 seconds but no stimulus was shown. The owner and the unknown person had been instructed not to move or interact with the dog during the course of the experiment.

The unfamiliar dominant dog was a four-year old male Belgian Shepherd Malinois and the degree of dominance was established by a professional dog trainer through specific behavioural tests [2]. The unfamiliar dog was located in a rectangular metal cage (120 cm x 150 cm x 90 cm)

between the white wall and the rectangular opening of the box. The cat used during the experiment was a four-year old European male whose owners had consented to participate in the experiment. The cat was located in a small metal cage (60 cm x 80 cm x 60 cm) in the same position as with the dominant dog.

Stimuli were presented in randomised order to different dogs two days per week (only two stimuli per day were shown to prevent habituation). Ten presentations (sessions) for each stimulus were given overall, covering a period of testing of 25 days.

Tail wagging scores associated with the different stimuli were analyzed from video-recordings. Positions of the tail were scored every 10 seconds by superimposition on the computer screen of a cursor on the long axis of the body: the maximum extents of the particular tail wag occurring at each 10 second interval was recorded. Using single frames from video recording two angles were identified with respect to the maximum excursion of the tail to the right and to the left side of the dog's body (Figure 1). Tail wagging angles were obtained with reference to the axes formed by the midline of the dog's pelvis — the segment extending lengthwise through the dog's hips, drawn from the largest points as seen from above; dotted line in Figure 1 — and the axes perpendicular to it.

Tail wagging angles were evaluated by the segment that extended lengthwise through the base and the tip of the tail, considering the tip of the sacral spine as 180° and the base of the tail as 0° (as in Figure 1). Minimal movements of the tail, within a range of maximum 3° overall, which were plausibly not correlated to wagging, were discarded.

The general analysis of variance is reported in the caption to Figure 2. When faced with their owner (Figure 2A), dogs exhibited a striking right-sided bias in the amplitudes of tail wagging ($F(1,28) = 33.036$, $p < 0.00001$). A similar striking bias was observed when dogs were shown an unfamiliar human being (Figure 2B; $F(1,28) = 21.569$, $p = 0.00007$), though with an overall decrease in the amplitude of tail wagging. When faced with a cat, dogs showed very reduced tail wagging movements, but still there was a slight bias favouring the right side (Figure 2C; $F(1,28) = 5.216$, $p = 0.030$). In contrast, when tested alone (Figure 2D; $F(1,28) = 6.041$, $p = 0.020$) or in the presence of an unfamiliar conspecific (Figure 2E; $F(1,28) = 6.836$, $p = 0.014$) dogs showed a left-sided bias of tail wagging.

It is noteworthy that the direction of the bias did not simply reflect the strength of wagging behaviour: a significant bias in the same direction (to the right) was observed with high (owner), medium (unknown human being) and very low (cat) amplitudes of tail wagging. Overall, this pattern of results fits with the general hypothesis that there is a fundamental asymmetry in the control of functions related to emotion.

Davidson [3] suggested that the anterior regions of the left and right hemispheres are specialised for approach and withdrawal processes, respectively. Although Davidson's hypothesis was developed in the context of human neuropsychology, approach and withdrawal are fundamental motivational dimensions which may be found at any level of phylogeny [4].

In our experiment, stimuli that could be expected to elicit approach tendencies, such as seeing a dog's owner, were associated with higher amplitude of tail wagging movements to the right side (left brain activation) and stimuli that could be expected to elicit withdrawal tendencies, such as seeing a dominant unfamiliar dog, were associated with higher amplitude of tail wagging movements to the left side (right brain activation). (As to the cross-over of descending motor pathways, in dogs the rubrospinal tract is the predominantly volitional pathway from the brain to the spinal cord; the pathway decussates just caudal on the red nucleus and descends in the controlateral lateral funiculus; fibres of the rubrospinal tract terminate on interneurons at all levels of the spinal cord; see [5].)

How far asymmetric tail-wagging responses are associated with postural asymmetry in preparation to the stimuli is difficult to say. It is likely that control of the flexure of the vertebral column is the same for the tail as well as the rest of the column, but the method we used for scoring tail-wagging responses and the panels flanking the body of the animal in the test-cage (Figure 1) minimized any effect of asymmetric posture associated with spine bending. Other postural asymmetries, such as head turning, which might bring the ear and eye of one side to bear more than the other could be associated with, or the cause of, asymmetry in the control of flexure of the vertebral column.

These findings with dogs add to mounting evidence for brain lateralization in a variety of nonhuman animals [6,7]. Such prominent behavioural asymmetries could be profitably used in dogs' welfare and veterinary behavioural medicine as a simple, non-invasive method to estimate quantitatively positive–negative emotions elicited by a variety of stimuli.
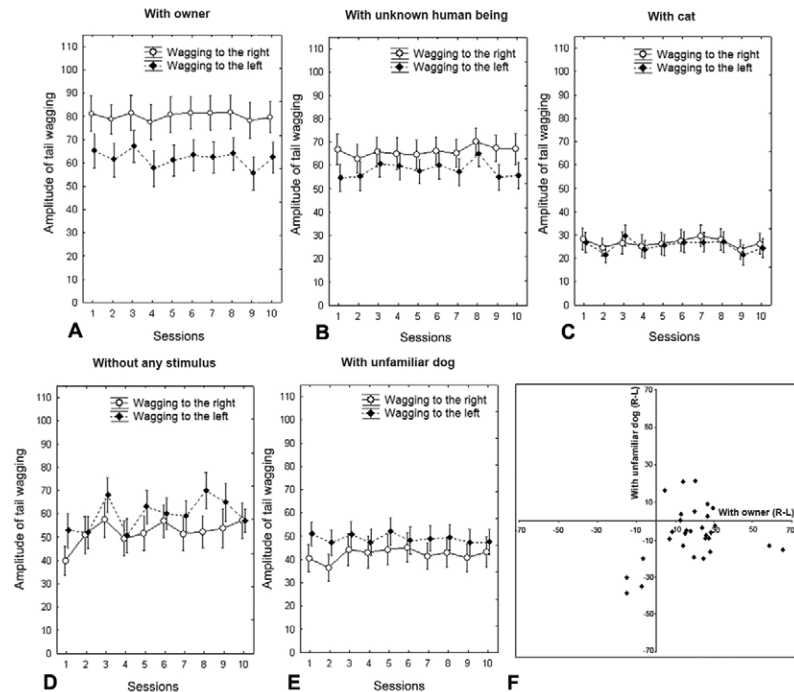

Figure 2. Amplitudes of tail wagging (degrees) to the left and right side when dogs were looking at different stimuli.

An analysis of variance with sex as a between-subjects factor, and stimulus conditions, sessions and right-left direction of tail wagging as within-subjects factor revealed significant main effects of stimulus conditions ($F_{(4,112)}$ = 17.036, $p < 0.00001$) and sessions ($F_{(9,252)}$ = 2.949, $p = 0.002$), as well as a significant stimulus conditions x right-left direction of wagging interaction ($F_{(4,112)}$ = 27.678, $p < 0.000001$). Given that there were no other statistically significant effects, data for males and females are lumped together, and separate analyses were done for each stimulus condition (see text). A significant right bias in wagging behaviour was observed with the owner (A), the unfamiliar human being (B) and the cat (C); a significant left bias was observed in the absence of stimuli (D) and with the unfamiliar dominant dog (E). A sample of data from individual animals is given in (F), showing a scattergram of a right–left (difference) score for each dog, with the 'With owner' condition on one axis and the 'With unfamiliar dog' on the other axis.

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