

Finally, since the vagus nerve has bidirectional control over the brain and the body, reactivation of sensory/visceral afferences might have enhanced brain activity within a body/brain closed loop process. Our study demonstrates the therapeutic potential of vagus nerve stimulation to modulate large-scale human brain activity and alleviate disorders of consciousness.

SUPPLEMENTAL INFORMATION

Supplemental Information contains one figure, one table, experimental procedures, additional discussion, and can be found with this article online at <http://dx.doi.org/10.1016/j.cub.2017.07.060>.

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How birds outperform humans in multi-component behavior

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Recent years have witnessed an astonishing flurry of studies demonstrating that some bird species show higher-order cognitive processes on par with primates [1–3]. As birds have no neocortex, cortical processing cannot be a requirement for higher order cognition [1,4]. Although birds have more neurons than expected from their small brain weights [5], their absolute neuron count is still lower compared to cortical neuron numbers of primates. How, then, is it possible that pigeons reach performance levels in, for example, abstract numerical competence and orthographic processing, that are comparable to that of macaques [6]? While the subpallium is very similar, the organization of the pallium differs tremendously between birds and mammals [1]; moreover, the avian pallium is characterized by small, extremely tightly packed neurons [5]. It is conceivable that signal processing could be faster in such a brain as a result of a higher speed of propagation of activation between neighboring assemblies, resulting in faster switch times between neighboring networks and neuronal representations of behavioral goals. This is important, as behavioral goals in real-life situations are often achieved by a series of sub-tasks [7,8], and especially when sub-tasks supersede each other and show little overlap in processing resources, neocortical (pallial) structures are involved [7,8]. We now report that pigeons are on par with humans when a task demands simultaneous processing resources; importantly, pigeons show faster responses than humans when sub-tasks are separated such that fast switches between processes are required.

To test such a proposition, a behavioral procedure is needed that: can be applied similarly to

birds and mammals; normalizes species-specific performance for simultaneous processing; and enables a quantitative analysis of behavioral switch speed. We used a Stop–Change task (SCT) with 15 humans and 12 pigeons (*Columba livia*; see Supplemental Information for details). The humans and pigeon subjects were required to perform a series of sub-tasks by stopping an ongoing response and then shifting to an alternative response (Figure 1A,B). This shift/change in responses was signaled either at the same time as the stop process with a STOP–CHANGE delay of 0 ms (SCD0), or with a short STOP–CHANGE delay of 300 ms (SCD300). In the SCD0-condition sub-tasks simultaneously demand processing resources — a condition that has been shown to be mediated via the basal ganglia [9]. In the SCD300-condition, however, sub-tasks were separated, resulting in a lower overlap of STOP and CHANGE-related processes, which has been suggested to be strongly mediated via cortical/pallial structures [8].

Our results show that pigeons and humans did not differ in their reaction times (RTs) on trials where an ongoing response was not interrupted (GO trials) ($t(25) = -0.03$; $p > 0.9$) (Figure 1C). Regarding the SCD trials, there were longer RTs in the SCD0 than in the SCD300 condition ($F(1,25) = 223.81$; $p < 0.001$; $\eta^2 = 0.9$), which is generally observed in that paradigm [8] because two response options simultaneously demand processing resources in the SCD0 condition, but less so in the SCD300 condition [8]. Importantly, there was an interaction ‘SCD condition x species’ ($F(1,25) = 21.76$; $p < 0.001$; $\eta^2 = 0.465$). As expected, post-hoc tests show that there were no RT differences between humans and pigeons in the SCD0 condition ($t(25) = 0.47$; $p > 0.6$; Figure 1C), which heavily relies on basal ganglia processes [9]. This behavioral finding nicely reflects the high structural similarity of the basal ganglia between birds and mammals [1]. Importantly, in the SCD300 condition pigeons showed ~200 ms faster RTs than humans ($t(25) = 3.05$; $p = 0.002$; Figure 1C). This behavioral pattern is validated by a further experiment to support

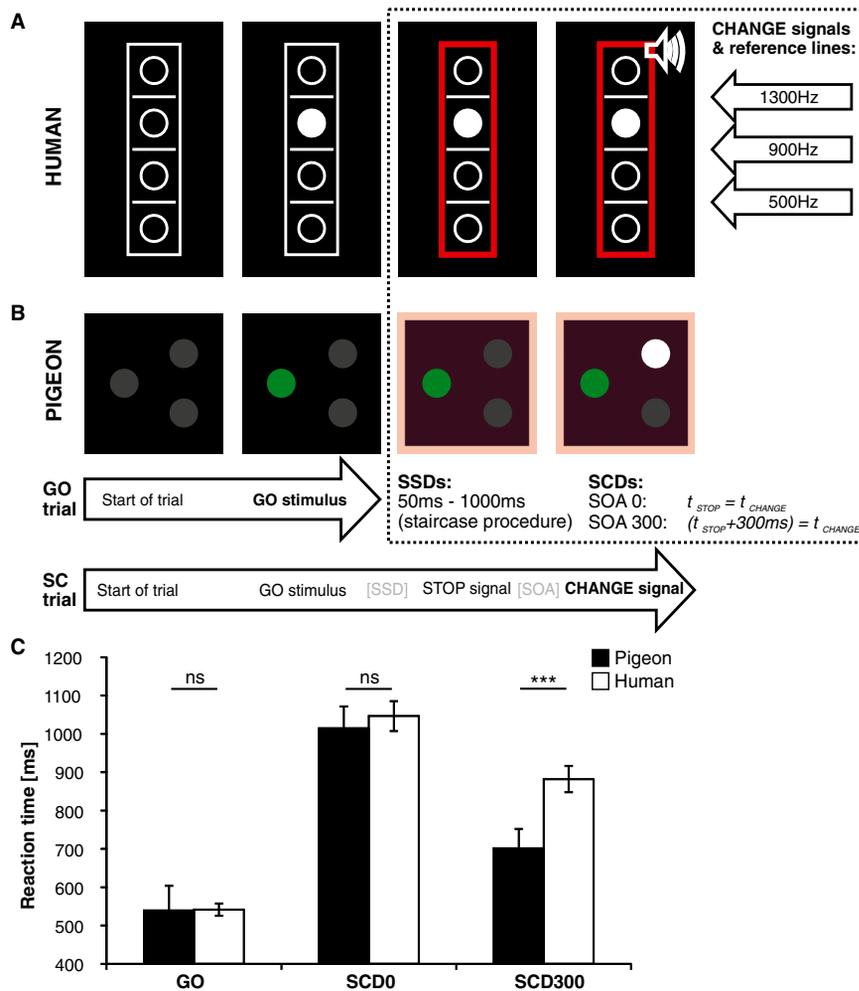


Figure 1. Schematic illustration of the Stop-Change paradigm and the corresponding reaction times for humans and pigeons.

(A) Schematic illustration of the Stop-Change paradigm for humans. A response to the GO stimulus (white circle) terminated GO trials while responses to the CHANGE stimulus terminated Stop-Change (SC) trials. The stop signal delay (SSD) between the GO stimulus and the STOP signal (red frame around circles and reference lines) was adjusted by means of a staircase procedure. The stop change delay (SCD) between the onset of the STOP and CHANGE stimuli was fixed and set to 0 ms in half of SC trials and to 300 ms in the other half. The three CHANGE stimuli were associated with one of the three reference lines (top right). (B) Schematic illustration of the Stop-Change paradigm for pigeons. As with the human paradigm, responding to the GO stimulus (left green circle) terminated the GO trial while responding to the CHANGE signal (right white circle) terminated the SC trials. The SSD was adjusted by means of a staircase procedure, identical to the human paradigm. The SCD intervals were also identical to the human paradigm. (C) Reaction times of humans and pigeons in the GO, SCD0 and SCD300 condition. Error bars represent standard errors of the mean (SEM). Asterisks indicate significant difference ($p = 0.002$).

the comparability of human and pigeon data despite differences in the physical experimental setup (Supplemental Experiment 1). A second experiment was conducted underlining that in humans and pigeons similar processing mechanisms are activated despite differences in the experimental setup (Supplemental Experiment 2).

The lack of behavioral differences between species in the GO and SCD0 trials was further confirmed using Bayesian analyses of the data (see Supplemental Information for details).

Our Stop-Change paradigm allowed us to conduct the same task under highly comparable conditions in humans and pigeons. Since we normalized performance

levels in terms of identical accuracy (see Supplemental Information for details), and there were no differences between species in the SCD0-condition, the faster reaction times of the pigeons in the SCD300-condition are strong evidence for a species-specific advantage to rapidly switch between sub-tasks (see Supplemental Information for details). In humans, simultaneous (SCD0) and cascaded processes (SCD300) mainly rely on basal ganglia and cortical circuits, respectively [7–9]. If conditions in birds are similar, the differently organized bird pallium should enable faster switches between neighboring representations of cascaded actions. Indeed, single unit recordings in the bird pallium show that cellular representations of response alternatives can often be found in close proximity [10]. It is conceivable that one of the reasons for the astonishing cognitive properties of birds is their high speed of switching between pallial assemblies. This functional property could be a consequence of their miniaturized pallium with high neuronal densities. Inter-neuron distances are on average 1.82 times smaller in pigeons compared to humans (see Supplemental Information for details), possibly enabling fast activation propagation between neighboring assemblies. This then could represent a key advantage of the non-cortical avian telencephalon over a cortical forebrain.

SUPPLEMENTAL INFORMATION

Supplemental Information includes experimental procedures and analysis, two further experiments, an additional discussion and two figures and can be found with this article online at <http://dx.doi.org/10.1016/j.cub.2017.07.056>.

AUTHOR CONTRIBUTIONS

S.L. conducted the experiments, analyzed the data, wrote the manuscript; O.G. conceived the experiments, wrote the manuscript; C.B. conceived the experiments, analyzed the data, wrote the manuscript.

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Whether European eel leptocephali use the Earth's magnetic field to guide their migration remains an open question

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European eels (*Anguilla anguilla*) migrate between the southwestern Sargasso Sea and the European and Mediterranean coasts. In a recent paper in *Current Biology*, Naisbett-Jones *et al.* [1] claim to “provide the first evidence that they [eels] derive positional information from the Earth's magnetic field” and that this information guides their migration. The evidence reported by Naisbett-Jones *et al.* [1] in support of this conclusion was derived from eels collected in the Severn River (UK), approximately 50 km upstream of the estuary (i.e. not “in the Severn Estuary” as stated by the authors). Eels collected this far into rivers are benthic and fully adapted to freshwater; that is, they are late-stage glass eels (~ 2 years old), not the pelagic leptocephalus (larval) life stage that actually undertakes the trans-Atlantic migration. The entire interpretive framework for the Naisbett-Jones *et al.* [1] study rests on the assumption that the behaviour of these late-stage freshwater glass eels, and their responses to magnetic fields, can be used as a proxy for the responses of eel leptocephali. The authors present no evidence in support of this key assumption.

The eel leptocephalus is a true larval form. It has completely different morphology, musculature, organ systems and behaviour from the other eel life-stages [2]. These differences are so striking that the leptocephalus larva was long believed to be a different species (*Leptocephalus brevirostris*). Late-stage glass eels display very specific behavioral patterns focused on their upstream migration in freshwater [3]. Their behavioural patterns and responses are adapted to a distinct set (and range) of environmental factors different from those of leptocephali. Thus, it is unrealistic to expect the eels studied by the authors to behave in the same way as leptocephali.

The authors' interpretations imply an additional assumption: that exposure to magnetic fields associated with the Sargasso Sea trick late-stage glass eels into thinking that they are back in the middle of the Atlantic Ocean when they are actually inland, in freshwater and at a higher temperature. We argue that a more parsimonious explanation is that the contradictory mixture of inappropriate physical and geomagnetic signals confused the late-stage glass eels, thereby explaining the “substantial variation in orientation among individuals” [1].

In addition to the unsubstantiated assumptions made about equivalence of life-stages, the study has several other critical flaws. The experiments of Naisbett-Jones *et al.* [1] were conducted in orientation arenas filled with 15 cm of freshwater, at 26°C, i.e. conditions very different from what eel leptocephali would encounter during their trans-Atlantic migration. During the test, glass eels were observed escaping from a central compartment into one of twelve peripheral chambers — this was the behaviour that was used by the authors to indicate orientation. Importantly, to move from the central compartment to one of the chambers, the eel had to crawl out of the water. Crawling out of the water is not something that a pelagic leptocephalus larva would ever do. For these reasons, we contend that the observations made by the authors to assess orientation cannot be