the abundance of mural-precursor cells allowed efficient recruitment and investment of mural cells to the engineered vessels, thereby enhancing their stability.

The vascular permeability of the engineered vessels is higher than that of normal, quiescent vessels, but is in the lower range of permeability values induced by various angiogenic molecules (see supplementary information). As in normal microcirculation, arteriolar and venular sides of the engineered vessels are readily identified by the pattern of blood flow. Local administration of a vasoconstrictor, endothelin-1, prompted constriction of the engineered arterial vessels. The few surviving arterioles in the HUVEC-alone constructs were significantly less contractile than those in the combined constructs (see supplementary information). These results indicate that the vessels that formed in the co-implantation construct have a better functionality.

Engineered blood vessels have often been found to be immature and unstable[6]. Genes that enhance the survival and/or proliferation of vascular cells — endothelial cells and mural cells — can be introduced to extend the lifespan of the engineered vessels[5,7,8], but these may prove to be oncogenic. We have created long-lasting blood vessels without such genetic manipulation.

In addition to realizing a crucial step in tissue engineering, our system provides a platform for testing the *in vivo* functions of factors that control angiogenesis, vasculogenesis and vessel maturation. The likely existence of endothelial and of smooth-muscle progenitor cells in adults[9,10] indicates that these cells might serve as a source of autologous cells for engineering blood vessels by using the approach described here.

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Animal behaviour

Inequity aversion in capuchins?

Brosnan and de Waal[1] have shown that capuchin monkeys are more likely to reject a cucumber slice after seeing that another capuchin has received a more attractive grape. In interpreting this finding, the authors make a link to work in humans on 'inequity aversion' and suggest that capuchins, like humans, may reject rewards because they are averse to unequal pay-offs. Here I argue that this interpretation suffers from three problems: the results contradict the predictions of the inequity-aversion model that Bosnan and de Waal cite[2]; experimental results indicate that humans do not behave like capuchins in similar circumstances; and the available evidence does not suggest that inequity aversion is cross-culturally universal[3–5].

I consider these points in turn. Brosnan and de Waal link their findings to work showing that a wide range of experimental behaviour in humans can be understood by introducing a preference for equity into the standard self-interested utility function. The effect of introducing this non-selfish preference is to cause individuals — under certain circumstances — to give up some of their pay-off in order to decrease the gains of other individuals.

Applying the Fehr–Schmidt inequity-aversion model[2] cited by Brosnan and de Waal to the capuchin experimental situation predicts that capuchins should always eat the cucumber. It does not predict that inequity-averse individuals will reject the food reward, which is what the monkeys did. Rejecting the cucumber increases, not decreases, inequality. Moreover, the grape-receiving capuchins sometimes reached through the cage and stole their partner's discarded cucumber, exacerbating the inequality.

Consistent with inequity aversion in humans, the results from experimental variations of the ultimatum game suggest that humans would not reject a reward unless that rejection reduced the take of the individual who received more. In the ultimatum game, two players are allotted a sum of money to divide. The first player — the 'proposer' — must offer a portion of the sum to the second player — the 'responder' — who must then decide whether to 'accept' or 'reject' the offer. If the responder accepts, he gets the amount of the offer and the proposer receives the remainder. If he rejects, both players get zero. The game is played once, and players never learn their partner's identity. Inequity aversion can explain the willingness of responders to reject low offers (in contrast, pure self-interest predicts that responders will never reject any non-zero offer). Once some responders are willing to reject low offers, self-interest guarantees that proposers will raise their offers.

Two kinds of variation from the standard ultimatum game suggest that humans, unlike capuchins, would not reject in Brosnan and de Waal's experimental context. Two versions of a reduced-form ultimatum game have been compared[6]: the first was a standard game, except that proposers had only two choices, an equitable allocation or a highly inequitable one; and the second (the 'impunity game') was identical, except that if the responder rejected his offer, the proposer's pay-off remained unchanged (but the responder received zero). In the first version, players were willing to reject inequitable allocations, whereas in the second version (which parallels the capuchin situation), subjects never rejected.

Similar evidence comes from multilateral ultimatum games in which one proposer faces multiple responders (see U. Fischbacher, C. M. Fong & E. Fehr, www.iew.unizh.ch/wp/iewwp133.pdf). In this set-up, as long as one of the responders accepts the offer, the proposer gets his pay-off. As before, the responder's ability to affect the proposer's pay-off by rejecting is mitigated by the other responders who might accept. As predicted by inequity aversion, responders decrease their willingness to reject, and proposers drop their offers accordingly. Therefore, although both of these experimental patterns are consistent with inequity aversion, both also seem to be at odds with Brosnan and de Waal's capuchin findings: that is, they show that humans will not reject unless this affects the other's pay-off.

Brosnan and de Waal also suggest that inequity aversion is probably a human universal, and they cite work that uses the ultimatum game in 15 small-scale societies[3–5]. If responder behaviour (willingness to reject low offers) is taken as the most direct measure of inequity aversion, then our results do not support the universal claim. Although five societies do show evidence consistent with inequity aversion, three others show evidence of trivially little or no inequity aversion. The remainder have so few low offers that no substantial claims can be made.

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