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NOTES & COMMENTS

Time to elaborate on some of Scholander's ideas: Does even a rudimentary form of the response of diving mammals exist in humans?

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Dear Sir

On page 16 of his excellent historical and ecological review, Hagen (2018) summarizes the view of Scholander's 1962 Harvey Lecture that

> compared to seals…human's ability to survive underwater was quite unremarkable. Nonetheless humans.. shared the same fundamental response to asphyxia found in their diving relatives- if only in a rudimentary form

But if humans share it even in a rudimentary form, why can't they hold their breath anywhere near as long as seals?

Most humans can hold for only ~1 min with a maximum lung inflation of air, with no hyperventilation and while resting (Parkes 2006). Whereas seals hold for ~30 min (Scholander et al. 1962) with a submaximal lung inflation of air, with no hyperventilation and while exercising (hunting). Surely, it is time to consider the better answer is that humans can't because they don't share the same fundamental response!

Scholander & Irving's magnificent work (Scholander 1940; Irving et al. 1942) showed that part of the fundamental response enabling seals to breath-hold for so long is to shut down blood supply to the intestines, muscles and other tissues (except the brain) to prevent oxygen uptake, i.e., to lower metabolic rate. Doing this with their ongoing level of cardiac output would cause a catastrophic rise in blood pressure. So they have a secondary response, which is to reduce cardiac output from 40 to 6 L min^{-1} (Zapol et al. 1979), by simultaneously reducing stroke volume and heart rate [cardiac output falling from 40 to 6 L min^{-1} and heart rate from 52 to $\leq$15 beats per minute (bpm)].

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Isaac Newton said that

> If I have seen further it is by standing on the shoulders of Giants.

We now have had sufficient time to evaluate Scholander's great work more fully. We have the benefit of subsequent knowledge that he did not have. There are two important but subtle points that Scholander very understandably appears not to have quite appreciated.

First, he, and many others subsequently e.g., Schmidt-Nielsen (1987), characterized the principal characteristic of the diving response as reducing heart rate. Possibly because heart rate is just too easy to observe. Whereas it is now clear to us that the principal characteristic is the shutting down of blood supply. The decrease in cardiac output is only secondary. I can find no explicit statement that Scholander appreciated this subtle distinction and his frequent surprise (Irving et al. 1942; Scholander et al. 1962) that

> in spite of the bradycardia the arterial blood pressure [in seals], is maintained at a normal level

indicates otherwise.

Secondly, Scholander had the preconception that humans must have the diving response of seals. He then interpreted his data to fit this. This is obvious from the text (Scholander et al. 1962) he uses (see his page 189) to describe heart rate in 31 Trochus divers (whose dives "….rarely exceeded 1 minute…").

He interprets his figure 1, without undertaking any numerical analysis, as showing the diving bradycardia of seals. In fact, the range of heart rates during breath-hold diving were between ~25 and 89 bpm (not the ~15 bpm of seals), and you can choose "control" values anywhere between ~61 and 128 bpm!

His interpretation appears universally and uncritically accepted in the scientific literature.

Moreover Scholander wished to take bradycardia even further as a grander generalisation as a common physiological mechanism shared by all vertebrates in a wide range of eco-physiological contexts. Addressing this generalisation is beyond the scope of this short commentary which solely concerns humans. It is left to others for a substantial review of its physiological ecology.

Nevertheless numerous numerical studies of human heart rates during breath-holding with immersion and while resting show that in all subjects there is a large range and that it does not consistently go to much below about 50 bpm (Lin 1982; Butler and Woakes 1987).

It is a cardinal sin in physiology to equate heart rate with cardiac output (without also measuring stroke volume). Equally, it cannot be the case every time heart rate falls in humans that a rudimentary diving response has been initiated. Operation of the baroreflex is an obvious exception. There also remain unresolved issues in establishing a proper control condition to measure the baseline heart rate (taking into account the normal respiratory sinus arrhythmia and the effect on heart rate of the last and large lung inflation before the breath-hold) to establish whether ~50 bpm represents a real (i.e.,. statistically significant) fall or just no change.

Agreed, in a few subjects, e.g., Ferrigno et al. (1991) there are descriptions of heart rates during diving of even lower heart rates (~30 bpm). But there are no controls for subject selection criteria, depth, posture, exercise intensity,water temperature and breath-hold duration. The alternative question here is why hasn't every study consistently reproduced this heart rate level?

Furthermore, if humans are immersed at a low enough water temperature (the typical temperature of the water in which seals dive), the cold shock response causes their heart rate to rise! (Tipton 1989). In any event, obsession over establishing the precise heart rate change during breath-hold diving in humans misses the key point. A heart rate fall is not the fundamental response of diving mammals.

Not only do humans fail to hold their breath as long as seals, but there is no evidence yet that humans can shut down peripheral blood supply completely during breath-holding while immersed, nor greatly reduce cardiac output in this condition to much below normal resting levels of ~5 L min^{-1} (which they would have to do if there was an undiscovered shutting down of peripheral blood flow).

I wish only to build on the seminal and scholarly work of Scholander, Irving et al., on the diving response in seals. And it was Jacob Bronowski who said that

> students…. are not here to worship what is known but to question it.

Surely it is time to consider the better answer to why humans cannot hold their breath anywhere near as long as seals is because they just don't share the same fundamental response!

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