Influence of Feeding and Exercise on the Distribution of Intestinal and Muscle Blood Flow in Ponies

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Summary

Cardiovascular changes associated with feeding in humans, dogs, cats, primates and sheep indicate the amount of blood distributed to the gastrointestinal tract increases following ingestion of a meal. This increased blood supply to the gastrointestinal tract can be provided by and increase in cardiac output, a redistribution of regional blood flow or by a combination of both these mechanisms. During submaximal exercise conducted in a postprandial state, dogs are able to maintain digestive tract blood flow, while primates divert blood away from the digestive system. In recent experiments using ponies, feeding has resulted in mesenteric hyperemia. Further, ponies exercised at 75 percent of heart rate maximum for 30 minutes 1.4 hours after feeding had higher digestive tissue and muscle blood flow compared to fasted ponies. This increased blood supply to both the digestive system and working muscles in fed ponies was accomplished by increases in heart rate, cardiac output, stroke volume and arterial blood pressure during exercise.

Einfluß von Fütterung und Bewegung auf die Blutverteilung in Verdauungskanal und Muskulatur bei Ponys

Kardiovaskuläre Veränderungen im Anschluß an die Nahrungsaufnahme – bei Menschen, Hunden, Katzen, Affen und Schafen – deuten auf eine postprandial verstärkte Durchblutung des Magendarmtraktes hin. Die erhöhte Blutversorgung des Verdauungskanals wird ermöglicht durch einen Anstieg des Herzminutenvolumens, eine Rückverteilung des peripheren Blutflusses oder durch ein Zusammenwirken beider Mechanismen. Postprandiale, mäßige Bewegungsbelastung führt bei Primaten zu einer Minderung der Magendarmdurchblutung, während Hunde in der Lage sind, den Blutfluß im Verdauungskanal aufrechtzuhalten. In neueren Versuchen mit Ponys führte die Fütterung zu einer Hypermämie des Darmgekröses. Im Vergleich zu nüchternen Tieren zeigten Ponys, die 1,4 Stunden nach der Futteraufnahme für 30 Minuten bewegt wurden (Herzfrequenz: 75 % des Maximums) eine stärkere Durchblutung von Darm- und Muskelgewebe. Diese erhöhte Blutversorgung von Verdauungssystem und Muskulatur wird erreicht durch eine Erhöhung von Herzfrequenz, Herzminutenvolumen und Schlagvolumen sowie des arteriellen Blutdrucks während der Bewegung.

Introduction

In an effort to link diet with equine exercise performance, many studies have evaluated differences in performance associated with manipulation of various dietary ingredients. However, these experiments fail to answer many fundamental questions including: What is the cardiovascular effect of simply feeding the animal, and what is the cardiovascular response to postprandial exercise?

Specific information regarding the distribution of blood flow within the digestive tract in fasted and fed horses is limited. Furthermore, information comparing the distribution of blood flow in fasted and fed horses during exercise is limited. Therefore, the objective of this paper is to briefly review the cardiovascular changes associated with feeding and exercise in other animals and then to detail a recent series of experiments to determine these same responses in ponies.

Cardiovascular response to feeding

The cardiovascular system of many animals responds to feeding in two distinct phases: 1) the anticipation/ingestion phase and 2) the postprandial phase *(Chou,* 1983). The anticipation/ingestion phase refers to the period when the animal is aware of an upcoming feeding and continues during ingestion of food. The postprandial phase refers to the period following ingestion of food. Research into the cardiovascular effect of feeding has concentrated primarily on changes in four response variables: heart rate (HR), cardiac output (CO), arterial blood pressure (ABP) and blood flow (BF) distribution. Changes in these variables will be discussed for both the anticipation/ingestion phase and the postprandial phase of feeding.

Anticipation/Ingestion. The cardiovascular system begins to react to feeding once the animal receives visual and/or auditory stimuli associated with feeding. *Fronek* and *Stahlgren* (1968) and *Vatner* et *al.* (1970 a, b) reported that anticipation/ingestion of food by dogs caused significant increases in CO, HR, and ABP, compared to fasting control measurements, made with the same dogs. Similar cardiovascular changes have been reported in calves, lambs and kids (*Bloom* et *al.*, 1975), adult sheep (*Christopherson* and *Webster*, 1972), primates (*Vatner* et *al.*, 1974) and adult humans (*Yi* et *al.*, 1990). The mechanism, for the cardiovascular changes which occur during anticipation/ingestion, appears to be activation of the sympathetic nervous system (*Chou,* 1983).

Postprandial. The postprandial period in calves, lambs and kids is characterized by a gradual decline, toward initial resting values, for both ABP and HR (*Bloom* et *al.*, 1975). Using dogs as an experimental model, *Fronek* and *Stahlgren* (1968) and *Vatner* et *al.* (1970 a, b) concluded that CO, HR and ABP had returned to pre-feeding control values by one-hour following a meal. Furthermore, *Vatner et al.* (1970 a, b) concluded these cardiovascular variables remain at control levels for up to seven hours postprandial, provided the dogs continued to rest.

Blood flow distribution (BF)

BF within the body is controlled by two mechanisms. It is controlled centrally through the nervous system, and locally by the metabolic activity of the tissue in the immediate vicinity of the blood vessels (*Astrand* and *Rodahl*, 1977). Blood is distributed and redistributed to the various tissues of the body by a combination of central and local control of arteriolar smooth muscle. In response to physical or emotional stress, various vascular beds within the body increase their metabolic activity. The increased BF demands of metabolically active tissue can be satisfied by an increase in CO, a redistribution of regional BF or by a combination of both these mechanisms (*Yi* et *al.*, 1990). Feeding is a common, but less recognized, activity capable of causing cardiovascular adaptations.

Anticipation/Ingestion. Reports concerning changes in BF during this phase of feeding are limited. Summarizing data from dogs (*Fronek* and *Stahlgren*, 1968; *Vatner* et *al.*, 1970 a, b; and *Kato* et *al.*, 1989) and primates (*Vatner* et *al.*, 1974) the anticipation/ingestion phase of feeding is characterized by a small decrease in mesenteric and renal BF, an increase in left gastric artery and coronary BF and variable changes in skeletal muscle BF.

Postprandial. The amount of blood distributed to the gastrointestinal tract increases following ingestion of meal. This postprandial mesenteric hyperemia has been reported in cats (*Fara* et *al.*, 1972), dogs (*Burns* and *Schenk*, 1969; *Fronek* and *Fronek*, 1970; *Bond* et *al.*, 1979 and *Gallavan* et *al.*, 1980), primates (*Vatner* et *al.*, 1974; and *Vatner*, 1978) and lambs (*Edelstone* and *Holzman*, 1981). Data also indicate that during digestion, BF increases in the area of the gut which is exposed to digesta, and not in other portions of the gastrointestinal tract (*Fara* et *al.*, 1972; *Chou* et *al.*, 1976; and *Gallavan* et *al.*, 1980). BF to the limbs and skeletal muscle has been reported to decrease (*Vatner* et *al.*, 1970 b and 1974) or remain unchanged (*Edelstone* and *Holzman*, 1981) during the postprandial phase of digestion, depending on physical activity of the subject. BF through other peripheral vascular beds (brain, kidney and heart) is not altered during digestion (*Gallavan* et *al.*, 1980; and *Edelstone* and *Holzman*, 1981).

Cardiovascular response to exercise

The cardiovascular effect of exercise has been studied in many different animals under a variety of exercise conditions. From these studies, it is apparent that during exercise great demands are made on a variety of muscles. This increased metabolic activity of muscle tissue leads to increased blood flow (*Astrand* and *Rodahl*, 1977). Two sources are available to supply the extra quantity of blood required by exercising muscle: 1) augmented total cardiac output and 2) redistribution of blood from regional beds.

Fixler et *al.*, (1976) and *Musch* (1987 a, b) concluded that as dogs increase exercise intensity, BF increases to the respiratory, cardiac and locomotive musculature. Meanwhile, BF decreases to the stomach, small intestine and large intestine and remains unchanged to the kidneys (*Fixler* et *al.*, 1976; and *Musch* 1987 a, b). These changes in canine BF during exercise are accompanied by increased HR and CO. Cardiovascular adaptations to exercise also have been studied in horses. In general, equine subjects increase HR, CO and ABP in proportion to running speed (*v. Engelhardt*, 1977; and *Thomas* and *Fregin*, 1981). As exercise intensity increases in ponies, BF decreases in the kidneys, increases in the muscular portion of the diaphragm, increases in exercising muscle and remains unchanged to the brain (*Parks* and *Manohar*, 1983 a). In a similar study, *Manohar* (1986 a) reported that BF in the kidneys, spleen, pancreas, small intestine and colon decreased precipitously during maximal exertion. Meanwhile, each of the major muscles involved in propulsion and respiration registered very large increases in BF during maximal exercise.

Cardiovascular response to postprandial exercise

The cardiovascular response to postprandial exercise has received limited research attention. *Jones* et *al.* (1965) reported that adult humans had significantly higher HR during postprandial exercise compared to exercise conducted in the fasted state. *Burns* and *Schenk* (1969), *Fronek* and *Fronek* (1970) and *Vatner* et *al.* (1970 a) each reported that dogs maintain postprandial mesenteric hyperemia during exercise. In baboons, feeding was associated with an increase in mesenteric blood flow(postprandial mesenteric hyperemia), but excitement reversed this vasodilation (*Vatner*, 1978).

Recently, experiments were carried out using ponies to address the following objectives: 1) determine hemodynamics and BF distribution during fasting (basal) conditions, 2) determine postprandial hemodynamics and BF and 3) compare hemodynamics and BF in fed and fasted animals during exercise.

Material and Methods

Sixteen pony geldings, ranging in age from 2 to 7 years and weighing 168 ± 15 kg (mean ± SEM), served as experimental animals. The ponies were equally divided into two dietary treatment groups: A) Fasted and B) Fed. Both groups were fed alfalfa hay (free-choice) throughout the study except during the 24 hours preceding data collection when the respective dietary treatments were imposed (see: Experimental Protocol). The ponies were exercise conditioned during a 45-day pretrial period. On the day of the study, the ponies were catheterized (left ventricle, thoracic aorta, right atrium) for determination of hemodynamics and regional BF using the microsphere technique (*Manohar* et *al.*, 1992). At each step of the protocol (see: Experimental Protocol) ABP, HR, CO, stroke volume and tissue BF were determined (*Manohar* et *al.*, 1992; *Duren*, 1990). The entire procedure was carried out with careful hemodynamic monitoring (*Parks* and *Manohar* 1983 a, b, *Manohar*, 1986 a, b) such that all criteria for regional BF and CO determination by the microsphere method were satisfied.

Experimental Protocol. The fasted ponies did not receive feed during the 24 hours preceding data collection. The fed treatment group was provided free-choice alfalfa hay, water and salt during the 24 hours preceding data collection. In addition, these ponies were offered a 12 % crude protein, pelleted grain concentrate at a rate equal to 1.0 % of body weight on the morning of data collection. These ponies were allowed 30 minutes to consume the grain concentrate with data collection (resting measurement) beginning 60 – 90 minutes after feed removal. Following their respective dietary treatments, hemodynamic and regional BF measurements were determined simultaneously at each of the following stages.

A. Rest (control/baseline): Hemodynamic measurements were made on ponies standing quietly on a treadmill in an air-conditioned laboratory (20°C) when aortic, left ventricular, and pulmonary artery pressures had been stable for at least 15 to 20 minutes.

B. Exercise: Following control measurements, the ponies were trotted on a motor-driven treadmill for 30 minutes at a speed setting of 28 km/hour and an incline of 7 %. At 5, 15 and 26 minutes of exercise, hemodynamic measurements were made as described above.

At the end of the experiment, the ponies were deeply anesthetized with thiamylal sodium and exsanguinated (*Parks* and *Manohar,* 1983 b). Tissue samples from the digestive tract including the esophagus, non-glandular stomach, glandular stomach, duodenum, jejunum, ileum, cecum, right ventral colon, left ventral colon, left dorsal colon, right dorsal colon, small colon and rectum were removed. Samples of limb muscle tissue including gluteus medius, biceps femoris, vastus lateralis and triceps brachii, as well as other muscles including the longissimus dorsi and masseter were removed. Finally, respiratory muscles including costal diaphragm, crural diaphragm, external oblique abdominous and internal oblique abdominous were removed. Tissue samples were analyzed in methods outlined by *Manohar* et *al.* (1992). Tissue BF and CO were computed as previously described by Manohar (1986 a, b). Data were analyzed by analysis of variance techniques using the general linear model procedure of *SAS* (1986). A probability level of $P < .05$ was regarded as statistically significant.

Results

Hemodynamics and regional BF in fasted ponies at rest. HR, CO, ABP, and stroke volume did not differ from those previously reported in resting ponies. Digestive tissue BF was lowest in the esophagus and highest in the glandular stomach. In the small intestine, BF was the highest in the duodenum. In the large intestine, the cecum had the highest BF while the rectum had the lowest flow. BF to the ventral and dorsal regions of the colon were similar. The pancreas had BF values 2-fold greater than any digestive tissue. Kidney BF was high and locomotor muscle BF was low compared to digestive tissues. In respiratory muscles, BF was 5-fold greater in the inspiratory muscles than in expiratory muscles. BF to the inactive longissimus dorsi and masseter muscles was low.

Postprandial hemodynamics and regional BF in ponies. During the 24 hours preceding data collection the fasted ponies were not given feed. Meanwhile, the fed ponies were provided free-choice access to alfalfa hay, and consumed a pelleted grain concentrate (.71 % of body weight) 1.22 hours prior to data collection. Fed ponies had higher ($P < .05$) stroke volume compared to fasted ponies. No differences were observed in HR, CO or ABP. BF to the esophagus, non-glandular stomach and glandular stomach were not different between fasted and fed ponies. As a result of feeding, BF increased ($P < .05$) to the duodenum (81 %), jejunum (68 %), Ileum (40 %), cecum (78 %), right ventral colon (135 %), left ventral colon (98 %), left dorsal colon (79 %), right dorsal colon (77 %), small colon (79 %), pancreas (135 %) and kidney BF (53 %). Muscle BF was not different ($P > .05$) between fasted and fed ponies for any of the muscles sampled.

Hemodynamics and regional BF in fasted and fed ponies during exercise. Exercise began 24 hours postprandial in the fasted ponies and 1.4 hours postprandial in the fed ponies. HR increased ($P < .05$) during exercise for both groups of ponies; however, the magnitude of increase for HR was greater during the first 5 minutes of exercise in fed than fasted ponies. Exercise increased CO, ABP and stroke volume in both fasted and fed ponies. CO, ABP and stroke volume were consistently higher ($P < .05$) in fed than in fasted ponies during exercise. BF to the digestive tracts of both groups of ponies decreased ($P < .05$) during exercise, but fed ponies had higher ($P < .05$) BF to the esophagus, small intestine, cecum, ventral colon, dorsal colon and small colon compared to fasted ponies. BF to the pancreas decreased ($P < .05$) as a result of exercise in both treatment groups. Pancreatic BF was greater ($P < .05$) in fed than fasted ponies at rest and these differences declined during exercise. Renal BF during exercise decreased ($P < .05$) in both fasted and fed ponies, with BF remaining higher ($P < .05$) in fed than in fasted ponies. BF to the locomotor muscles increased ($P < .05$) during exercise in both treatment groups; however, BF was higher ($P < .05$) in fed than in fasted ponies. BF to the respiratory muscles and the longissimus dorsi increased ($P < .05$) during exercise in both treatment groups. As with the locomotor muscles, BF during exercise to the respiratory muscles and the longissimus dorsi was conistently higher ($P < .05$) in fed than in fasted ponies, although the magnitude of this difference varied. BF to the masseter was unchanged during exercise, and did not differ between fasted and fed ponies.

Discussion

Hemodynamics and regional BF in fasted ponies at rest. HR, CO, ABP and stroke volume did not differ from values previously reported in ponies (*Parks* and *Manohar,* 1983 a). Digestive tissue BF was lowest in the esophagus. This was expected since the muscle tissue in the esophagus is only active when a swallowing movement is initiated (*Swenson,* 1984). BF was higher in the glandular stomach than the non-glandular stomach. The glandular stomach secretes approximately 20 liters of gastric juice/day (*Frape,* 1986), potentially accounting for the high BF. Slightly lower stomach BF values have been reported for fasted dogs by *Kato* et *al.* (1989). The amount of BF to the small intestine is dependent on tissue oxygen demand, which is influenced by motility, absorption and secretion (*Norris* et *al.*, 1979). The fasted ponies had small intestines which were essentially devoid of digestive material. Therefore, the oxygen demand of, and tissue BF to, the small intestines was expected to be low. The 24-hour fast imposed in this study did not empty the large intestine of digestive material. As a result, the BF values obtained for the various segments of the large intestine do not represent an absolute fasting condition. *Manohar* (1986 b) reported higher resting pony colonic BF values. In canine studies, colonic BF values also exceeded those reported in this study (*Musch* et *al.*, 1987 a). However, comparison with Manohar's pony study and Musch's dog study is difficult since the feeding schedules of their animals were not reported. Due to the continuous nature of pancreatic secretion (*Swenson,* 1984), BF to the pancreas was expected to be high. Similar pancreatic BF values have been reported in ponies by *Manohar* (1986 a). BF values for the left and right kidneys were not different ($P > .05$), verifying adequate mixing of microsphere and blood. Locomotor muscle BF was similar to values reported by *Parks* and *Manohar* (1983 b). The 5-fold difference in resting BF between the diaphragm (principle muscles of inspiration) and the oblique muscles (principle muscles of expiration) was expected given the function of each muscle during breathing.

Postprandial hemodynamics and regional BF in ponies. BF to the esophagus and stomach was not different ($P > .05$) between fasted and fed ponies. *Kato* et *al.* (1989) reported that dogs increased left gastric arterial BF 270 % above fasting levels, immediately after the ingestion of food. However, this dramatic increase in BF lasted for only 10 minutes, despite the continued presence of food in the stomach (*Kato* et *al.*, 1989). If the pony stomach behaves similarly to that of the canine, the BF values measured 1.22 hours postprandial in this study, would not be expected to differ from fasting values. Data from this study indicate a postprandial mesenteric hyperemia throughout the small intestine and large intestine (excluding the rectum). Postprandial mesenteric hyperemia has been reported in humans (*Muller* et *al.*, 1990) primates (*Vatner* et *al.*, 1974) dogs (*Bond* et *al.*, 1979) cats (*Fara* et *al.*, 1972) and sheep (*Edelstone* and *Holzman,* 1981). *Chou* et *al.* (1976) concluded that chyme, and specifically the hydrolytic products of food digestion, play a major role in postprandial mesenteric hyperemia. The exact mechanism by which chyme in the lumen produces hyperemia are not clearly defined. One possible explanation is that chyme contacts the mucosa and causes the release of vasoactive hormones into circulation (*Granger* et *al.*, 1980). Another possible explanation is that chyme stimulates intestinal absorption, secretion and motor activities (*Granger* et *al.*, 1980). These processes increase cellular oxygen demand, and oxygen requirements are met by alterations in BF and/or oxygen extraction (*Granger* et *al.*, 1980). In this study, feeding resulted in a 135 % increase in pancreatic BF. Postprandial pancreatic hyperemia has not been reported previously for the pony; however, given the secretory function of the pancreas during digestion, functional hyperemia was expected. In dogs, pancreatic BF has been reported to double within 30 minutes after a meal (*Gallavan* et *al.*, 1980). In this study, BF to the kidney was higher in fed than in fasted ponies. It is hypothesized that fluid absorbed from the intestine during digestion is responsible for the postprandial increase in renal BF. In this study, there were no differences in muscle BF between fasted and fed ponies for any of the muscles sampled. *Fara* et *al.* (1972) using cats and *Edelstone* and *Holzman* (1981) using lambs each concluded that muscle BF was not changed as a result of feeding. Studies which report a decrease in muscle BF concurrently with postprandial mesenteric hyperemia all conclude that animals must remain totally inactive during the postprandial period to see the change in BF (*Vatner* et *al.*, 1970 a, 1974). In the present study, the ponies were not totally inactive after feeding.

Hemodynamics and regional BF in fasted and fed ponies during exercise. BF through the entire digestive tract decreased during exercise in both treatment groups. However, fed ponies maintained consistently higher BF to each of these tissues during exercise. In dogs, mesenteric hyperemia was maintained during submaximal exercise (*Vatner* et *al.*, 1970 a). *Manohar* (1986 b) reported a decrease in small intestine and colon BF in ponies during maximal exercise, although the feeding schedule was not given. Pancreatic BF decreased during exercise in both treatment groups during exercise. In fed ponies, pancreatic BF was much higher at rest but the differences during exercise were small. Similar decreases in pancreatic BF have been reported in dogs (*Musch* et *al.*, 1987 b) and in ponies (*Manohar,* 1986 b). Renal BF has been reported to be well-maintained during exercise in dogs (*Musch* et *al.*, 1987 b). In this study BF to the kidney decreased during exercise for both fasted and fed treatment groups; however, BF during exercise was higher in fed than in fasted ponies. BF to the locomotor and respiratory muscles increased during exercise in both treatment groups. However, the fed ponies had consistently higher BF to these muscles. HR, CO, ABP and stroke volume each increased during exercise in both treatment groups. The HR, CO, ABP and stroke volume responses during exercise were greater in the fed than in the fasted ponies. Pooling the BF results with the hemodynamic data, the fed ponies directed more blood to both the digestive system and working musculature. This was accomplished by an increased HR, CO and stroke volume at the given exercise intensity (approximately 75 % of HR maximum).

Conclusion

Experiments conducted using many different animal models indicate there is a cardiovascular effect associated with feeding. This cardiovascular effect is evident by changes in cardiac performance and BF distribution. In recent experiments, BF in fasted ponies was found to be the lowest in the esophagus and rectum, two tissues devoid of absorption capabilities. Digestive tissue BF was highest in the glandular region of the stomach followed by the duodenum, two tissues with large secretory capacity. Feeding resulted in mesenteric hyperemia, evident by increased BF to the small intestine, cecum, ventral colon, dorsal colon, small colon, pancreas and kidney. BF to locomotor and respiratory muscles was not affected by feeding. During treadmill exercise (75 % HR maximum), fed ponies (1.4 hours postprandial) distributed an increased amount of blood to both the digestive system and working musculature. This increased blood supply was provided by higher HR, CO, ABP and stroke volume in fed compared with fasted ponies.

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