CHAPTER 7

STUDY 4

Off-transient $\dot{V}O_2$ and mOxy responses following moderate-, heavy- and severe-intensity exercise in well-trained young and middle-age cyclists

OVERVIEW

The purpose of Study Four was to examine the effect of age on the off-transient $\dot{V}O_2$ and mOxy responses following moderate-, heavy- and severe-intensity SWT in well-trained cyclists. The results of Study Four suggest no significant effect of age on the off-transient $\dot{V}O_2$ or mOxy responses of well-trained cyclists. This absence of a significant effect of age may be explained by the similar relative SWT intensities, $\dot{V}O_2$max and/or muscle histochemical and enzymatic characteristics of the two age groups.

The results of Study Four demonstrated significant effects of intensity in the end-exercise amplitude (EE$\dot{V}O_2$), A_f, and τ_f of the $\dot{V}O_2$ response. In addition, significant effects of intensity were also observed in the off-transient EEmOxy and mOxy A_f. Furthermore, a small number of significant relationships were observed between the off-transient $\dot{V}O_2$ and mOxy responses and several hematological measures taken at the completion of the three SWT intensities. This study also observed several significant relationships between the off-transient $\dot{V}O_2$ and mOxy responses and the muscle histochemical and enzymatic characteristics of the well-trained cyclists. Therefore, the major finding of Study Four was the absence of a significant effect of age in the off-transient $\dot{V}O_2$ or mOxy responses following the three SWT intensities in well-trained matched cyclists.

RESULTS

Off-Transient $\dot{V}O_2$ Responses

Table 7.1 over the page summarises the off-transient $\dot{V}O_2$ kinetic parameters for each age group across the three SWT intensities.

No main effect of age or age x intensity interaction was observed for the EE$\dot{V}O_2$ in the present study. However, a significant increasing main effect of intensity ($F(2,24)=187.613$, $p<0.001$, $\eta^2=0.940$) was observed on the EE$\dot{V}O_2$. RMANOVA revealed a similar effect in the separated young ($F(2,12)=106.62$, $p<0.001$, $\eta^2=0.947$) and middle-aged ($F(2,12)=84.631$, $p<0.001$, $\eta^2=0.934$) cyclists. In the young cyclists, the EE$\dot{V}O_2$ for the heavy- ($F(2,12)=106.62$, $p<0.001$, $\eta^2=0.947$) and severe-intensity ($F(2,12)=106.62$, $p<0.001$, $\eta^2=0.947$) exercise was significantly higher than that following the moderate-intensity SWT. Similar findings were observed in the middle-aged cyclists between the EE$\dot{V}O_2$ of the moderate and heavy-intensity ($F(2,12)=84.631$, $p<0.001$, $\eta2=0.934$) SWT, as well as the severe-intensity ($F(2,12)=84.631$, $p<0.001$, $\eta^2=0.934$) SWT.

Table 7.1: Mean (± SD) time and amplitude values of the off-transient $\dot{V}O_2$ response of the young and middle-aged cyclists following the three square wave transition intensities.

	Young			Middle-Aged		
	Moderate	**Heavy**	**Severe**	**Moderate**	**Heavy**	**Severe**
$EE\dot{V}O_2$ (mL•min^{-1})	2469 ± 363	3487 ± 510 #	3405 ± 418 §	2623 ± 239	3648 ± 345 #	3636 ± 363 §
A_f (mL•min^{-1})	1468 ± 287	2288 ± 375 #	2147 ± 305 §	1581 ± 254	2398 ± 308 #	2318 ± 370 §
TD_f (s)	17.9 ± 4.8	20.3 ± 7.5	16.8 ± 6.5	14.5 ± 5.4	19.7 ± 3.5	15.4 ± 6.5
τ_f (s)	35.3 ± 5.3	41.2 ± 5.0	52.5 ± 11.9 §	35.0 ± 7.9	40.8 ± 6.7	56.7 ± 16.8 §
$wMRT_f$ (s)	53.2 ± 6.5	61.5 ± 10.9	69.3 ± 6.0 §	49.5 ± 9.3	60.5 ± 7.4	72.1 ± 18.2 §

$EE\dot{V}O_2$ = End-exercise $\dot{V}O_2$
A_f = Off-Transient Amplitude
TD_f = Off-Transient Time Delay
τ_f = Off-Transient Time Constant
$wMRT_f$ = Off-Transient Weighted Mean Response Time

significant difference between moderate and heavy-intensities ($p<0.05$); § significant difference between moderate and severe-intensities ($p<0.05$).

No significant effect of age or age x intensity interaction was observed on the $\dot{V}O_2$ A_f in the present study. However, a significant main effect of intensity (F(2,24)=81.906, p<0.001, η^2=0.872) was observed for the $\dot{V}O_2$ A_f. The $\dot{V}O_2$ A_f was significantly different in both the young and middle-aged cyclists between the moderate and heavy-intensity SWT [Y: (F(2,12)=62.813, p<0.001, η_2=0.913); MA; (F(2,12)=30.865, p=0.001, η^2=0.837)], as well as between the moderate and severe-intensity SWT [Y: (F(2,12)=62.813, p<0.001, η^2=0.913); MA: (F(2,12)=30.865, p<0.001, η^2=0.837)]. Furthermore, the $\dot{V}O_2$ A_f was significantly correlated to the $\dot{V}O_2$ A_p of the heavy-intensity SWT (r= 0.92, p= 0.03) in the young cyclists, but not in the middle-aged cohort (r= -0.37, p= 0.41).

No significant main effects of age, intensity or age x intensity interaction were observed for the $\dot{V}O_2$ TD_f in the young and middle-aged cyclists. Moreover, no significant main effect of age or age x intensity interaction was observed in the $\dot{V}O_2$ τ_f. However, a significant main effect of intensity (F(2,24)=12.406, p<0.001, η^2=0.508) was observed for $\dot{V}O_2$ τ_f which was demonstrated in the separated young (F(2,12)=6.794, p=0.011, η^2=0.556) and middle-aged subjects (F(2,12)=6.058, p=0.015, η^2=0.561). The moderate-intensity $\dot{V}O_2$ τ_f was significantly shorter than the values measured during the severe-intensity SWT in both the young (F(2,12)=6.794, p=0.027, η^2=0.556) and middle-aged (F(2,12)=6.058, p=0.022, η^2=0.561) cyclists.

No significant effect of age or age x intensity interaction was observed for $\dot{V}O_2$ $wMRT_f$. However, a significant main effect of intensity (F(2,24)=7.223, p=0.004, η^2=0.376) was observed for $\dot{V}O_2$ $wMRT_f$. A significant effect of intensity ($F(2,12)=4.736$, $p=0.030$, $\eta^2=0.441$) was only observed in the $\dot{V}O_2$ $wMRT_f$ of the middle-aged cyclists. *Post-hoc* analysis revealed that the moderate- and severe-intensity $\dot{V}O_2$ $wMRT_f$ were significantly different ($F(2,12)=4.736$, $p=0.037$, $\eta^2=0.441$) in this cohort.

Off-Transient mOxy Responses

The off-transient mOxy kinetics for all three SWT intensities are summarised in Table 7.2 over the page.

No significant main effect of age or age x intensity interaction was observed for the EEmOxy. However, a significant main effect of intensity in the EEmOxy was observed in both the young ($F(2,11)=49.295$, $p<0.001$, $\eta^2=0.891$) and middle-aged ($F(2,11)=31.295$, $p<0.001$, $\eta^2=0.862$) cyclists.

While no significant main effect of age was observed for mOxy A_f, a significant age x intensity interaction was observed for the mOxy A_f ($F(2,22)=10.139$, $p=0.001$, $\eta^2=0.480$). A significant main effect of intensity ($F(2,22)=10.139$, $p=0.001$, $\eta^2=0.480$) was observed for the mOxy A_f. *Post-hoc* analysis revealed significant differences between the moderate and severe-intensity exercise in the young cyclists ($F(2,11)=4.062$, $p=0.041$, $\eta^2=0.448$), and the moderate- and heavy-intensity SWT in the middle-aged cyclists ($F(2,11)=9.232$, $p=0.001$, $\eta^2=0.606$). Similar to the $\dot{V}O_2$ response, the mOxy A_f was significantly correlated to the on-transient mOxy A_p in both the young ($r= 0.92$, $p= 0.01$) and the middle-aged ($r= 0.91$, $p= 0.004$) cyclists following the heavy-intensity SWT.

Table 7.2: Mean (± SD) time and amplitude values of the off-transient mOxy response of the young and middle-aged cyclists following the three square wave transition intensities.

	Young			Middle-Aged		
	Moderate	**Heavy**	**Severe**	**Moderate**	**Heavy**	**Severe**
EEmOxy (%)	59.7 ± 14.1	31.0 ± 19.9 #	7.8 ± 8.4 § ¥	66.5 ± 10.5	35.6 ± 12.2 #	23.6 ± 13.5 § ¥
A_f (%)	30.6 ± 14.0	39.2 ± 17.8	41.5 ± 16.1 §	25.0 ± 8.9	49.6 ± 10.7 #	32.3 ± 15.0
TD_f (s)	5.2 ± 2.0	5.6 ± 2.0	5.1 ± 1.8	5.3 ± 1.0	6.4 ± 3.9	4.3 ± 1.5
τ_f (s)	39.5 ± 10.5	42.4 ± 14.2	43.5 ± 9.3	34.2 ± 26.3	38.7 ± 9.1	43.4 ± 3.7
A_{fs} (%)			26.1			27.5 ± 1.4
TD_{fs} (s)			62.8			67.5 ± 2.7
τ_{fs}s)			18.6			20.3 ± 2.0
$wMRT_f$ (s)	44.7 ± 10.1	48.0 ± 14.1	46.9 ± 25.1	36.5 ± 26.2	39.5 ± 26.2	80.2 ± 42.2 §

EEmOxy= End-exericse mOxy
A_f = Off-transient Amplitude
TD_f = Off-transient Time Delay
τ_f = Off-transient Time Constant
A_{fs} = Slow Off-transient Amplitude
TD_{fs} = Slow Off-transient Time Delay
τ_{fs} = Slow Off-transient Time Constant
$wMRT_f$ = Off-Transient Weighted Mean Response Time

significant difference between moderate and heavy-intensities ($p<0.05$); § significant difference between moderate and severe-intensities ($p<0.05$); ¥ significant difference between heavy and severe-intensities ($p<0.05$); N.B: No off-transient slow component was observed for the moderate or heavy-intensity SWT.

No significant main effect of age, intensity or age x intensity interaction was observed in the mOxy TD_f, τ_f or $wMRT_f$ in the present study. However, the mOxy TD_f was found to be significantly shorter than the $\dot{V}O_2$ response in both age groups following all three SWT intensities.

Correlations between $\dot{V}O_2$ and mOxy kinetics and hematological variables

Significant correlations between the $\dot{V}O_2$ and mOxy off-transient kinetics and the hematological variables are shown in Table 7.3.

Correlations between $\dot{V}O_2$ and mOxy kinetics and muscle histochemical and enzymatic characteristics

Significant correlations between the muscle histochemical and enzymatic characteristics and the off-transient $\dot{V}O_2$ kinetic parameters are shown in Table 7.4a. Significant correlations observed between all the muscle histochemical and enzymatic characteristics and the off-transient mOxy kinetic measures are listed in Table 7.4b.

Table 7.3: Correlation coefficients (r) for the relationships between the amplitude and time parameters of the off-transient $\dot{V}O_2$ responses following the moderate-, heavy- and severe-intensity square wave transitions and changes in hematological parameters in the young and middle-aged cyclists.

Young				Middle-Aged			
		r	**p**			**r**	**p**
			Moderate-Intensity				
$\dot{V}O_2$ τ_f	$[HCO_3^-]$ @ 6 min	-0.91	0.005	$\dot{V}O_2$ MRT_f	pO_2 @ 6 min	-0.86	0.014
	$[BLa^-]$ @ 6 min	0.79	0.033		$[HCO_3^-]$ @ 6 min	-0.73	0.003
	$[BLa^-]$ Δ3-6 min	0.79	0.034				
$\dot{V}O_2$ MRT_f	$[BLa^-]$ @ 6 min	0.77	0.041				
	$[BLa^-]$ Δ3-6 min	0.86	0.013				
			Heavy-Intensity				
				$\dot{V}O_2$ A_f	$[HCO_3^-]$ @ 6 min	0.77	0.043
				$\dot{V}O_2$ τ_f	$[HCO_3^-]$ Δ3-6 min	0.76	0.049

Table 7.4a: Correlation coefficients (r) for the relationships between the amplitude and time parameters of the off-transient $\dot{V}O_2$ responses following the moderate-, heavy- and severe-intensity square wave transitions and histochemical and enzymatic characteristics of the young and middle-aged cyclists.

Young				Middle-Aged			
		r	p			r	p
Type IIa %	Heavy τ_f	0.78	0.037	Type I %	Severe $EE\dot{V}O_2$	0.84	0.032
Capillary Density	Heavy $EE\dot{V}O_2$	-0.76	0.048	Type I CSA	Heavy MRT_f	0.95	0.005
	Heavy A_f	-0.78	0.037	Type IIa %	Heavy MRT_f	0.84	0.036
CS activity	Moderate $EE\dot{V}O_2$	-0.78	0.043	Type IIb %	Heavy A_f	-0.96	0.002
	Heavy $EE\dot{V}O_2$	-0.80	0.030		Severe A_f	-0.81	0.049
	Heavy A_f	-0.77	0.045	Type IIb CSA	Heavy MRT_f	0.89	0.018
	Severe $EE\dot{V}O_2$	0.87	0.011	Capillary Density	Heavy MRT_f	-0.82	0.025
	Severe A_f	-0.84	0.017				

Table 7.4b: Correlation coefficients (r) for the relationships between the amplitude and time parameters of the off-transient mOxy responses following the moderate-, heavy- and severe-intensity square wave transitions and histochemical and enzymatic characteristics of the young and middle-aged cyclists.

Young				**Middle-Aged**			
		r	**p**			**r**	**p**
Type I %	Heavy τ_f	0.82	0.044	PFK Activity	Moderate TD_f	-0.85	0.016
Type IIb %	Heavy MRT_f	-0.92	0.010				
	Severe MRT_f	-0.82	0.009				
Capillary Density	Severe EEmOxy	-0.82	0.046				
C:F Ratio	Severe τ_f	0.92	0.009				
CC/F	Severe τ_f	0.93	0.008				
	Severe $wMRT_f$	0.83	0.043				
DD_{max}	Severe τ_f	0.93	0.006				
	Severe MRT_f	0.82	0.048				
CS Activity	Moderate τ_f	0.84	0.034				
2-OGDH Activity	Moderate MRT_f	0.81	0.049				

DISCUSSION

The purpose of Study Four was to examine the effect of age on the off-transient $\dot{V}O_2$ and mOxy kinetics following moderate-, heavy- and severe-intensity SWT in well-trained cyclists. No effect of age was observed on the off-transient $\dot{V}O_2$ or mOxy responses in the well-trained cyclists in the present study.

Little data has been published examining the recovery kinetics of the concurrent off-transient $\dot{V}O_2$ and mOxy responses following three different exercise intensities (Puente-Maestu et al. 2003; duManoir et al. 2005). Few studies have examined the effect of age on these physiological recovery responses. From the available research, the rate of metabolic recovery following an exercise bout appears to be slowed with sedentary aging (Chick et al. 1991; Chilibeck et al. 1997; Ichimura, Murase, Osada, Kime, Homma, Ueda, Nagasawa, Motobe, Hamaoka and Katsumura 2006). In contrast, it has recently been suggested that the off-transient $\dot{V}O_2$ and mOxy responses are improved with physical activity, despite aging (Ichimura et al. 2006). Therefore, the current study is the first to provide data on the effect of concurrent aging and physical training on the off-transient $\dot{V}O_2$ and mOxy responses following moderate-, heavy- and severe-intensity exercise.

The present study demonstrated no significant effect of age on the off-transient $\dot{V}O_2$ or mOxy responses examined following the three SWT intensities in the well-trained cyclists. The absence of a significant effect of age on the off-transient responses is most likely the result of the matching of the two age groups on their physiological characteristics (e.g. $\dot{V}O_2max$, muscle histochemical characteristics) as reported in Study One. Furthermore, the similar hematological responses and relative SWT intensities reported in the earlier studies of the present series of investigations may also help to explain the absence of an effect of age on these responses (Borsheim and Bahr 2003).

The present findings both support and contrast a range of previously reported effects of exercise intensity on the off-transient $\dot{V}O_2$ and mOxy responses (Bahr and Sejersted 1991; Bahr 1992; Borsheim and Bahr 2003; Puente-Maestu et al. 2003). The current data demonstrated significant effects of intensity in both the end-exercise amplitude and A_f in both the $\dot{V}O_2$ and mOxy responses within both age groups. Similarly, the $\dot{V}O_2$ τ_f and $wMRT_f$, as well as the mOxy TD_f significantly lengthened across increasing exercise intensities. To date, few studies have reported upon the effect of age on the concurrent off-transient $\dot{V}O_2$ and mOxy responses following various exercise intensities (Puente-Maestu et al. 2003; duManoir et al. 2005).

Off-Transient Amplitude Responses

The off-transient $\dot{V}O_2$ and mOxy responses help to quantify and model the return of energy metabolism to baseline values within the working muscle cell following exercise (Bahr and Sejersted 1991; Bahr 1992). In the present study, no significant effects of age were observed in either the $\dot{V}O_2$ or mOxy end-exercise amplitude ($EE\dot{V}O_2$; EEmOxy) or A_f for any of the three SWT intensities. The absence of any significant effect of age within the two groups may reflect the similar physiological and muscle characteristics observed in the two age groups examined in the present series of studies.

Given the curvilinear $\dot{V}O_2$-Work relationship observed across increasing exercise intensities (Barstow et al. 2000), the off-transient $\dot{V}O_2$ and mOxy amplitude measures were expected to, and did demonstrate, a significant increase with exercise intensity in the present study. A similar effect was observed in both the $\dot{V}O_2$ and mOxy on-transient responses in both age groups. This increase with higher exercise intensities on the off-transient $\dot{V}O_2$ and mOxy amplitude measures reflects the increasing energetic demands of the three SWT and supports the suggestion that exercise intensity and duration are major influencing factors on the off-transient response (Borsheim and Bahr 2003). Furthermore, the matching of physiological and muscle histochemical and enzymatic characteristics of the present study's cohorts and relative SWT intensities may be responsible for the observed similarities in the off-transient A_f in the present study. The observation of similar increases in the off-transient $\dot{V}O_2$ and mOxy A_f in each age group is suggestive of greater magnitude of recovery following each SWT intensity. It further suggests that the off-transient responses may be dependent upon either the physiological characteristics of the cyclists or the intensity or duration of the exercise task, and that physical training with aging attenuates any such effect of age on these responses.

Off-Transient Speed Responses

The speed of the off-transient response refers to the path that the $\dot{V}O_2$ and mOxy measures take when returning to baseline levels following the completion of an exercise bout (Gaesser and Brooks 1984; Bahr 1992; Borsheim and Bahr 2003). The results of the present study revealed no significant effect of age on the off-transient speed measures (TD_f; τ_f) of the $\dot{V}O_2$ and mOxy responses in the well-trained cyclists. The absence of a significant effect of age on these off-transient responses is in contrast to that previously reported for older sedentary populations (Chick et al. 1991; Ichimura et al. 2006).

The present data revealed no significant effect of age on the $\dot{V}O_2$ or mOxy TD_f in the well-trained cyclists. Further, a stable $\dot{V}O_2$ TD_f across the three SWT intensities may suggest that the intra-muscular signalling time required for the decrease in energy metabolism is independent of exercise intensity (Hanada, Okita, Yonezawa, Ohtsubo, Kohya, Murakami, Nishijima, Tamura and Kitabatake 2000). The mOxy TD_f was significantly shorter than the $\dot{V}O_2$ TD_f in both the young and middle-aged cyclists across the three separate SWT intensities in the present study. This difference between the responses suggests that intra-muscular reoxygenation and recovery mOxy kinetics occur faster than proposed through the $\dot{V}O_2$ measures observed at the mouth. This discrepancy between the two physiological measures may reflect the instantaneous measurement of mOxy, and the actual monitoring of the reoxygenation of the Hb and Mb stores within the working muscle by the NIRS technology. The $\dot{V}O_2$ TD_f may be lengthened due to the transit time of deoxygenated blood from within the muscle to the lungs, as well as the reoxygenation of Hb stores outside the working muscles.

No significant effect of age was observed for the $\dot{V}O_2$ or mOxy τ_f or $wMRT_f$ in the present study. This absence of a significant effect of age in the $\dot{V}O_2$ and mOxy τ_f is consistent with the on-transient responses examined in Study Two of this series of investigations. Thus, the present study suggests that the off-transient $\dot{V}O_2$ and mOxy responses are not slowed with concurrent aging and physical training. This result may suggest that the nature of the off-transient $\dot{V}O_2$ and mOxy responses is dependent upon either $\dot{V}O_2max$ or the histochemical and enzymatic characteristics within the working muscle. These characteristics may have a strong influence on the utilisation of O_2 within the muscle following completion of an exercise bout. Interestingly, the two sedentary age groups described by Chilibeck et al. (1997) reported similar $\dot{V}O_2$ τ_f (Y: 33.1 ± 16.6 s; O: 44.1 ± 18.8 s) to that reported in the present investigation for moderate-intensity exercise (Y: 35.3 ± 5.3 s; MA: 35.0 ± 7.9 s). However, in comparing the off-transient $\dot{V}O_2$ and mOxy responses, previous research has reported that the $\dot{V}O_2$ τ_f (32 ± 5 s) occurs significantly faster than the mOxy response (91 ± 26 s) in young (27 ± 5 y) healthy males following moderate-intensity leg extension exercise (duManoir et al. 2005). The results of the present study are in contrast to this observation and suggest that the $\dot{V}O_2$ and mOxy τ_f were similar across the three SWT intensities. This suggests that the off-transient $\dot{V}O_2$ responses resemble that of the working muscle in terms of O_2 extraction and energetic costs. This difference between the current study and the results of duManoir et al. (2005) may have resulted from the different modes of exercise or training status of the subjects as both have been reported to influence the incurred metabolic demands of exercise and the nature of the off-transient response.

The present data are the first to examine the off-transient mOxy responses in well-trained young and middle-aged athletes following exercise bouts of increasing intensity. No significant effect of age or intensity was observed in the off-transient mOxy τ_f in the well-trained cyclists. The absence of a significant effect of age in the present study may suggest that the mechanisms responsible for metabolic recovery are controlled by several important physiological or muscle histochemical characteristics. This is further supported by the absence of a significant effect of intensity on the mOxy τ_f which again suggests that the controlling mechanisms lie within the working muscle and depend upon the capacity to utilise O_2 within the working muscle. Recently, Ichimura and colleagues (2006) reported that the mOxy $\tau½$ was significantly shorter in physically active, but not physically trained middle-aged (53 ± 5 y; 22.5 ± 3.3 s) and elderly (67 ± 5 y; 29.6 ± 8.9 s) subjects compared to a cohort of sedentary age-matched counterparts (MA: 50 ± 6 y; 35.7 ± 9.0 s; E: 66 ± 3 y; 45.7 ± 13.6 s). As such, the lack of difference between the experimental groups may be explained by the similar physiological capacities and muscle histochemical and enzymatic characteristics of the well-trained cyclists in the present study.

A significant lengthening effect of intensity was observed on the $\dot{V}O_2$ τ_f in the present investigation. In contrast, no such effect was demonstrated in the mOxy τ_f. The observation of a lengthened $\dot{V}O_2$ τ_f with increasing exercising intensity in the present study most likely reflects the greater energy metabolism and associated recovery processes within and outside the muscle with increased exercise intensity. The $\dot{V}O_2$ τ_f values from the present study (33-55 s) are similar to those observed in younger populations performing similar exercise intensities (Paterson and Whipp 1991; Engelen et al. 1996; Ozyener et al. 2001; Perrey, Candau, Borrani, Millet and Rouillon 2002). The lengthened $\dot{V}O_2$ τ_f with increasing exercise intensities observed in the present study contrasts previous research findings reporting a stable $\dot{V}O_2$ τ_f across exercise intensities (Paterson and Whipp 1991; Cunningham, Croix, Paterson, Ozyener and Whipp 2000; Ozyener et al. 2001), but agrees with others (Engelen et al. 1996; Billat et al. 2002) that have reported a slowed $\dot{V}O_2$ τ_f with increasing exercise intensities. The lengthened $\dot{V}O_2$ τ_f with increasing exercise intensities is suggestive of O_2 consuming influences that do not necessarily occur within the working muscle. This suggestion is supported by the observation of no effect of intensity on the mOxy τ_f in the present study. This significant lengthening of the $\dot{V}O_2$ τ_f may reflect metabolic processes such as lactate oxidation within non-active muscles that occurs with increasing exercise intensities given the required O_2 cost for conversion of lactate to pyruvate.

In contrast, the absence of a significant effect of intensity on the mOxy τ_f suggest that the speed of reoxygenation of the working muscle following exercise is not influenced by prior exercise intensity. The mOxy τ_f values reported in the present study across the three SWT intensities (35-45 s) appear faster than those reported previously by Puente-Maestu et al. (2003) for similar SWT intensities (~46-74 s) in chronic obstruction pulmonary disease patients. This difference in the mOxy τ_f may be due to the diseased nature of the cohort reported upon by these previous investigators. Puente-Maestu and colleagues (2003) demonstrated that the mOxy τ_f did not significantly lengthen with exercise intensity, either before or after a six week endurance-training regime. They did, however, report a significant improvement in the mOxy τ_f across all SWT intensities as a result of the exercise training. This training effect suggests that the speed of the off-transient mOxy response is controlled through peripheral mechanisms that control the rate of O_2 utilisation within the exercising muscle following an exercise bout.

The observed discrepancies in the off-transient $\dot{V}O_2$ and mOxy τ_f discussed above may be due to metabolic factors external to the working muscle associated with the measurement of changes in the $\dot{V}O_2$ responses determined at the mouth. The present study is the first to concurrently examine the off-transient $\dot{V}O_2$ and mOxy in a group of well-trained athletes across increasing exercise intensities. The results support the findings of Puente-Maestu and others (2003) of a significantly faster off-transient mOxy response compared to the $\dot{V}O_2$ response across increasing exercise intensities. The previous work of Puente-Maestu et al. (2003) demonstrated that the off-transient $\dot{V}O_2$ τ_f was much slower than that of the mOxy response following a constant-load exercise bout performed at 80% VT. It is proposed that this difference between the $\dot{V}O_2$ and mOxy τ_f may reflect the specific monitoring of metabolic recovery of the working muscle that requires O_2 utilisation as measured through NIRS technology. In contrast, while the $\dot{V}O_2$ response measured at the mouth is reflective of the recovery of the working muscle, it is also subject to influences from several metabolic processes outside the working muscle. These might include lactate oxidation within both active and non-active musculature, the metabolic cost of synergist and stabiliser muscles, and substrate oxidation (Bahr and Sejersted 1991; Bahr 1992). These factors and their effect on the off-transient responses will be discussed below.

Off-Transient Physiological Mechanisms

The present findings of a lengthening off-transient $\dot{V}O_2$ τ_f compared to the mOxy τ_f suggest that the physiological mechanisms that control the $\dot{V}O_2$ and mOxy recovery responses are different. This finding supports the previous suggestion that the off-transient $\dot{V}O_2$ response is slower than the mOxy response following an exercise bout (Puente-Maestu et al. 2003). The off-transient mOxy response characterises the replenishment of O_2 content within the working muscle and may not reflect additional physiological mechanisms that may contribute to a slowed $\dot{V}O_2$ recovery that occur outside the working muscle. The speed of the off-transient $\dot{V}O_2$ and mOxy responses appears to be influenced by several physiological mechanisms, located within and external to the working muscle (Gaesser and Brooks 1984; Bahr 1992; Borsheim and Bahr 2003). These external mechanisms may include Hb reoxygenation, PCr resynthesis, lactate oxidation or the additional energy cost of synergistic or stabiliser muscles (Gaesser and Brooks 1984; Bahr 1992; Puente-Maestu et al. 2003).

The resynthesis of intra-muscular PCr stores has long been suggested as a contributor to the metabolic recovery of the working muscle following an exercise bout (Brooks et al. 1971; Gaesser and Brooks 1984; Rose, Hodgson, Kelso, McCutcheon, Reid, Bayley and Gollnick 1988; Langsetmo and Poole 1999; Borsheim and Bahr 2003). Previous investigations have matched the on-transient $\dot{V}O_2$ response to the PCr kinetics at exercise onset (Barstow et al. 1994). Therefore, in order to metabolically recover, these PCr stores must be replenished following an exercise bout. This hypothesis is based on the suggestion that intra-cellular PCr reserves are consumed within the working muscle during the on-transient response until aerobic metabolism of ATP can match the requirements of the intensity of the exercise bout (Barstow et al. 1994). However, the resynthesis of PCr stores within the working muscle has been shown to account for only a small portion of the off-transient $\dot{V}O_2$ amplitude in both humans (<10%) (Brooks et al. 1971) and horses (<1.5%)

(Rose et al. 1988). More recently, Langsetmo and Poole (1999) suggested that if PCr resynthesis was the sole mechanism responsible for the off-transient $\dot{V}O_2$ response, then its recovery path would be identical to that of the on-transient response which has been reported to mimic PCr degradation kinetics (Rossiter et al. 1999). Therefore, it has been previously demonstrated that PCr resynthesis following moderate-, heavy- and severe-intensity exercise would have minimally contributed to the off-transient $\dot{V}O_2$ and mOxy responses. The discussed metabolic processes primarily refer to the restoration of a homeostatic environment.

A second factor that may influence the off-transient $\dot{V}O_2$ and mOxy responses is the reoxygenation of Hb and Mb stores originally deoxygenated at exercise onset (Grassi et al. 2003). It is proposed that the HbO_2 and MbO_2 stores within the working muscle act as a reserve of O_2 within the muscle to sustain aerobic metabolism until the delivery and utilisation of O_2 is increased to meet the energetic demands of the exercise bout (Mooren and Volker 2005). The HbO_2 and MbO_2 stores help to reduce the magnitude of O_2 deficit and anaerobic metabolism required at the onset of the exercise bout in order to meet its energetic demands. Therefore, following the completion of the exercise bout, the deoxygenated Hb and Mb stores are required to be reoxygenated, which is reflected through the TD_f of the $\dot{V}O_2$ and mOxy responses (Hanada et al. 2000). However, this reoxygenation occurs at the initial period of the off-transient response and therefore may not contribute to the overall speed of metabolic recovery within the muscle. The rate of $\dot{V}O_2$ and mOxy recovery responses is most likely controlled through other metabolic processes within and external to the working muscle such as lactate oxidation and PCr resynthesis (Borsheim and Bahr 2003).

Previous investigations have suggested that the off-transient response is strongly related to the concentration of several hematological parameters following exercise completion (Gaesser and Brooks 1984). This most likely reflects the role of O_2 utilisation in returning the muscle cell to metabolic homeostasis. In the present study, the $[HCO_3^-]$ was inversely related to both the $\dot{V}O_2$ τ_f and the $wMRT_f$ of the young and middle-aged cyclists, respectively. The importance of this relationship is reflected through the decreased $[HCO_3^-]$ buffering potential being related to a lengthened off-transient $\dot{V}O_2$ τ_f across the three SWT intensities. This observation suggests that a lengthened off-transient $\dot{V}O_2$ response is related to the greater anaerobic metabolism and $[H^+]$ accumulation within the working muscle during higher exercise intensities. Such processes have been suggested to play a role in the nature of the off-transient metabolic responses (Gaesser and Brooks 1984; Bahr 1992; Borsheim and Bahr 2003). The present data support this suggestion and also strongly links the nature of the off-transient $\dot{V}O_2$ and mOxy responses to $[BLa^-]$ at completion of the exercise bout.

Gaesser and Brooks (1984) have suggested that the oxidation of lactate within the muscle (active and non-active) and liver contributes to metabolic recovery following high-intensity exercise. It has been suggested that the fate of lactate following high-intensity exercise influences the nature of the off-transient $\dot{V}O_2$ response (Gaesser and Brooks 1984; Borsheim and Bahr 2003). In the present data, the off-transient $\dot{V}O_2$ τ_f was significantly related to the $[BLa^-]$ at the completion of the moderate-intensity SWT in the young cyclists, but not following the heavy or severe-intensity SWT in either age cohort. This is surprising, given the elevated [BLa$^-$] at the completion of the two high-intensity SWT in the present study. However, the absence of a significant relationship between the off-transient $\dot{V}O_2$ and mOxy responses and the [BLa$^-$] at the end of the supra-threshold SWT may be due the large variance in the [BLa$^-$] response of the two cohorts. Therefore, it may be that the actual influence of lactate removal on the off-transient $\dot{V}O_2$ and mOxy response is not yet fully understood.

Previous investigations have examined the fate of lactate following high-intensity exercise, with it being suggested that 75-90% of lactate is converted back to glycogen within working and non-working muscle following exercise (Hill and Lupton 1923; Gaesser and Brooks 1984). The oxidation of lactate within the muscle appears to be dependent upon the activity of gluconeogenic enzymes (e.g. Fructose-1, 6-diphosphatase) (Gaesser and Brooks 1984). The activity of this gluconeogenic enzyme is believed to vary between different muscle fibre types (Jobsis, Meijer and Vloedman 1976; Cutmore, Snow and Newsholme 1985; Tikkanen et al. 1995). Type II fibres are capable of intra-muscular gluconeogenesis using lactate at physiologically significant rates due to a higher activity of the relevant enzymes (Donovan and Pagliassotti 2000). This suggestion may be supported by the present study's significant correlation observed between the Type IIb fibre composition and off-transient heavy and severe-intensity $\dot{V}O_2$ and mOxy recovery responses in both the young and middle-aged cyclists. Given the various oxidative potential of the different muscle fibre types, it is likely that the influence of muscle histochemical characteristics is the utilisation of O_2 within the working muscle following an exercise bout.

The present data have suggested that the utilisation of O_2 within the muscle cell is the most likely mechanism for controlling the speed of the metabolic recovery within the working muscle. Whilst the role of O_2 utilisation during the off-transient $\dot{V}O_2$ recovery phase has been highlighted, the delivery of O_2 to the muscle has also been reported to influence the off-transient $\dot{V}O_2$ response (Hughson et al. 1991; Chilibeck et al. 1997). Chilibeck and colleagues (1997) reported that the off-transient $\dot{V}O_2$ τ_f following moderate-intensity plantar flexion exercise was significantly related to muscle capillarisation of the VL in young (~26 y) but not older (~66 y) sedentary subjects. These investigators suggested that the delivery of O_2 may be of great importance, given the larger O_2 gradients between blood and muscle following an exercise bout as compared to that during the on-transient $\dot{V}O_2$ response. It is likely that the shorter O_2 diffusion distances and greater streaming of O_2 into the muscle cells associated with increased capillarisation allows an increased O_2 utilisation within the mitochondria following exercise completion allowing faster recovery (Chilibeck et al. 1997). In the present study, significant correlations were observed between the capillary density and CS activity and the off-transient $\dot{V}O_2$ A_f in the young cyclists. The middle-aged cyclists only demonstrated a significant relationship between the capillary density and $\dot{V}O_2$ $wMRT_f$ following the heavy-intensity SWT. Thus, the similar peripheral muscle characteristics of the present study's well-trained cyclists, together with the widely varied individual off-transient $\dot{V}O_2$ and mOxy responses, make it difficult to identify the controlling factors of the off-transient responses in the present study.

In summary, the physiological basis of the off-transient response represents the metabolic recovery of the working muscle to baseline values following the completion of an exercise bout (Gaesser and Brooks 1984). The present data showed no significant effect of age in the off-transient $\dot{V}O_2$ or mOxy responses. This may reflect the similar physiological capacities, muscle histochemical and enzymatic characteristics and relative exercise intensities observed in the two groups investigated. The findings of the current study also suggest that exercise intensity has a significant effect on the amplitude of the off-transient $\dot{V}O_2$ and mOxy responses, as well as the speed of the off-transient $\dot{V}O_2$ response. As no effect of intensity was observed in the off-transient mOxy response, this suggests that the off-transient $\dot{V}O_2$ response is influenced by external metabolic processes following bouts of high-intensity exercise. The current consensus is that the elevated $\dot{V}O_2$ requirements following a bout of exercise are due to several intra-muscular recovery processes such as PCr resynthesis, Hb and Mb reoxygenation, lactate oxidation and substrate metabolism (Gaesser and Brooks 1984; Bahr 1992; Borsheim and Bahr 2003). Such factors appear to be the casual mechanisms that control the utilisation of O_2 within the working muscle, and determine the magnitude of metabolic recovery required after the completion of an exercise bout.

SUMMARY

The purpose of Study Four was examine the effect of age on the off-transient $\dot{V}O_2$ and mOxy responses following moderate, heavy and severe-intensity SWT in well-trained cyclists. No significant effects of age or age x intensity interactions were observed in the off-transient $\dot{V}O_2$ or mOxy responses in the well-trained cyclists. The absence of a significant effect of age in the off-transient responses examined within the present study reflects the similar physiological, muscle histochemical and enzymatic characteristics, as well as the similar relative exercise intensities used in the study by the two age groups.

In support of previous research findings, significant effects of intensity were observed in several off-transient $\dot{V}O_2$ and mOxy amplitude and speed measures (Bahr and Sejersted 1991; Langetsmo, Weigle, Fedde, Erickson, Barstow and Poole 1997; Langsetmo and Poole 1999; Billat et al. 2002; Borsheim and Bahr 2003; Puente-Maestu et al. 2003). The present study did not identify the controlling mechanisms of the off-transient $\dot{V}O_2$ or mOxy responses. However, the current study suggests that different mechanisms influence the nature of the off-transient $\dot{V}O_2$ and mOxy responses, as evidenced by the conflicting effect of intensity on both the off-transient $\dot{V}O_2$ and mOxy responses. This difference may suggest an influence of a number of O_2 consuming processes outside the working muscle on the off-transient $\dot{V}O_2$ response, but not in the off-transient mOxy response.

Thus, the results of the present study strongly suggest that the off-transient $\dot{V}O_2$ and mOxy responses are maintained into middle-age through physical training. The present data also suggest that the off-transient $\dot{V}O_2$ and mOxy responses are controlled through different physiological mechanisms. This was supported by several significant correlations between the off-transient $\dot{V}O_2$ and mOxy responses and a number of hematological and histochemical characteristics in both age groups. These similar relationships further support the absence of a significant effect of age in the nature of the off-transient responses and controlling mechanisms in the present study.