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Walking and Running on the Circular Treadmill: Transition Speed and Podokinetic Aftereffects

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Abstract

The author compared 10 participants' self-selected walk-to-run transition speeds on a standard treadmill with those on a circular treadmill. The speed of the outer limb at walk-to-run transition on the circular treadmill and on the standard treadmill were very similar. Adaptive aftereffects from running and walking on the circular treadmill were also similar. When asked to step in place without vision, all participants inadvertently turned in circles following walking or running on the treadmill. The results of the present study suggest that the mechanisms controlling walk-to-run transitions are similar for the standard and circular treadmills and demonstrate the robust generalizability of locomotor aftereffects from running to walking. Adaptive control of speed, form, and direction may therefore share similar mechanisms for walking and running.

Keywords

adaptation; gait; transition speed

Flexibility of locomotor control, whether it be changing direction, speed, or form of locomotion, is critical for daily navigation in changing environments. Changes in speed can trigger changes in locomotor form; for example, with increasing speed, individuals reach a point at which they transition from a fast walk to a slow run. Changes in locomotor trajectory are also essential for modifying walking direction. In this study, the author examined control of locomotor speed, form, and direction in walking and running by using a rotating treadmill to determine (a) whether there is a relationship between self-selected walk-to-run transition speeds on the circular treadmill and on a standard linear treadmill, (b) whether participants demonstrate adaptive changes in locomotor trajectory after running on the circular treadmill, and (c) whether those adaptive changes, if expressed, differ following running from those following walking on the circular treadmill.

The author first compared walk-to-run transition speeds on the circular treadmill with those on the standard linear treadmill. Walk-to-run transitions have been the topic of much research, and there are multiple hypotheses regarding the factors that influence walk-to-run transition speed. Several investigators have shown that the preferred transition speed is not the optimal transition speed in terms of overall metabolic costs of locomotion because people consistently choose to transition to a run at a lower speed than that which would be energetically optimal (Brisswalter & Mottet, 1996; Hreljac, 1993; Tseh, Bennett, Caputo, & Morgan, 2002). In fact, there is a substantial metabolic cost associated with the actual transition step (Usherwood & Bertram, 2003). Despite those findings, participants' perceived exertion is lower when running than when walking at the preferred transition speed (Hreljac).

Given that the self-selected walk-to-run transition speed is not optimal in terms of overall metabolic costs, other factors must contribute to the choice of transition speed. There is conflicting evidence regarding the role of limb length in determining transition speed. Some investigators have noted a poor ability to predict transition speed on the basis of limb length (Hanna, Abernethy, Neal, & Burgess-Limerick, 2000; Raynor, Yi, Abernethy, & Jong, 2002). However, the results of earlier work suggested that limb length may be a determinant of transition speed (Thorstensson & Roberthson, 1987). Limb length has been shown to be a good predictor of transitions in some situations (Getchell & Whitall, 2004). Limb length may limit the maximum spread that the lower limbs can achieve during walking. As that limit is approached, one may be forced to increase stride frequency and internal mechanical work at higher walking speeds; however, switching to a run may decrease internal work, even though stride frequency is higher in running than it is in walking (Minetti, Ardigo, & Saibene, 1994). The importance of limb length in determining transition speed remains an area of controversy.

Others hypothesize that transition speed is determined in large part by muscular factors. Both Hreljac (1995) and Prilutsky and Gregor (2001) proposed that the motor system may effect the walk-to-run transition to prevent overexertion of the tibialis anterior muscle. They posited that at high walking velocities, there is increased activation of tibialis anterior so that the increased joint moment demands can be met and the toe prevented from dragging. That high level of activity in tibialis anterior may lead to localized muscle fatigue, discomfort, and an exaggerated sense of effort. Switching to a run reduces the need for such high tibialis anterior activity because the individual then relies more on larger muscle groups of the upper legs and hips to assist with foot clearance. Neptune and Sasaki (2005), on the other hand, suggested that soleus force, length, and velocity properties may determine the walk-to-run transition speed. They noted that force output of the soleus decreased at speeds above 80% of preferred transition speed, a reduction they attributed to the force, length, and velocity properties of muscle. Switching to a run resulted in nearly doubled force production for similar levels of soleus activation. Still others have suggested that walk-to-run transitions are driven by inverted pendulum dynamics (Kram, Domingo, & Ferris, 1997), changes in stride length variability with increasing speed (Brisswalter & Mottet, 1996), and kinetic factors, such as loading rate (Raynor et al., 2002).

In all studies to date, researchers have examined walk-to-run transition speed on a standard treadmill. I wanted to determine walk-to-run transition speed on a circular treadmill and see how that speed compared with transition speed on a standard treadmill. I hypothesized that the speed of transition would differ between the circular and standard treadmills if maximum stride length is the main contributing factor, because the physical constraints of the rotating treadmill do not allow full stride length to be achieved. However, if muscular factors are the main determinants of walk-to-run transition, then transition speed on the rotating and standard treadmills would be closely related: The linear speed of the outer and more quickly moving limb at transition on the circular treadmill would be comparable with the speed of that limb at transition on the standard treadmill, assuming that similar movement patterns are used on the linear and circular treadmills.

In addition to walk-to-run transition speed, I was interested in comparing locomotor adaptations resulting from walking and from running on the circular treadmill. Aftereffects from walking on a circular treadmill have been the subject of study for the past decade. Following walking on a circular treadmill, participants asked to step in place or walk straight across the floor with eyes closed will inadvertently turn in circles. That effect is called *podokinetic after-rotation* (PKAR; Gordon, Fletcher, Melvill Jones, & Block, 1995; Weber, Fletcher, Gordon, Melvill Jones, & Block, 1998). PKAR is characterized by a rapid rise in turning velocity during the initial 2 min of the response (Weber et al.). The rising phase is thought to represent an interaction between the podokinetic and vestibular systems (Earhart,

Sibley, & Horak, 2004). The rise is followed by a decaying phase that is relatively free of vestibular influence and extends from minutes 2–30. As such, analysis of PKAR typically entails the use of two separate curve fits, one for minutes 0–2 and another for minutes 2–30 (Weber et al.). PKAR is a robust phenomenon that generalizes from forward to backward walking and from walking to hopping (Earhart et al., 2001, 2002b). To date, no investigators have examined the effects of running on the circular treadmill. I hypothesized that PKAR would be similar following running or walking on the circular treadmill at the transition speed. That notion is supported by the work of Li, van den Bogert, Caldwell, van Emmerik, and Hamill (1999), who showed that running and walking at transition speed have similar coordination patterns, and by previous work showing that treadmill speed, and not cadence or duration of foot contact with the rotating surface, is an important determinant of the PKAR response (Earhart & Horak, 2004).

Method

Participants

Ten healthy participants (9 women, 1 man; mean age = 23.6 ± 2.6 years) took part in this study. All participants provided informed consent before participating. Each participant completed 2 sessions that were separated by at least 24 hr. Participants were familiar with the rotating treadmill and had the opportunity to walk on it before the actual experimental sessions. The local Human Subjects Committee approved this study.

Data Collection

In the first session, each participant walked on a standard treadmill, beginning at a speed of 0.22 m/s and gradually increasing the speed in 0.04 m/s increments until reaching a speed at which he or she transitioned from a walk to a run. I denoted the speed at which the participant first ran as the participant's linear walk-to-run transition speed. For both Sessions 1 and 2, each participant then walked on the perimeter of a 1.2-m-diameter disc that began rotating clockwise at a speed of 30 deg/s and was gradually and continuously increased until the participant transitioned to a run. One must use continuous, gradual increases rather than test at distinct intervals of constant speed to elicit natural gait transition behavior, as evidenced by Li (2000) and Li and Hamill (2002). Participants had an area with a width of 52 cm in which to walk or run on the perimeter of the disc (see Figure 1). The custom-built circular treadmill (Neuro Kinetics, Inc., Pittsburgh, PA) was kept at that walk-to-run transition speed (i.e., the speed at which the participant first ran), and the participant either walked quickly or ran slowly at that speed for 15 min. Participants who walked during Session 1 ran during Session 2, and vice versa. I made distinctions between walking and running on the basis of visual observation and participant self-report. The circular treadmill speed was the same for the 15 min of walking or running in Sessions 1 and 2, and I determined randomly whether participants walked or ran first. It was necessary to keep the treadmill speed standard across both conditions because PKAR velocity is directly related to treadmill velocity, with higher PKAR velocity following locomotion at higher treadmill velocity (Weber et al., 1998).

Following the 15 min on the circular treadmill, participants were asked to step in place on the floor while wearing a blindfold and earplugs. Participants must use a blindfold to eliminate visual inputs because PKAR is overridden by visual inputs and is not expressed when a blindfold is not worn (Jürgens, Bob, & Becker, 1999). Participants used earplugs so that they could not use auditory cues to orient themselves. Participants attempted to step in place for 30 min to the beat of a metronome (2 Hz) affixed to the trunk. Cadence was standardized and controlled via a metronome because previous work has shown that PKAR velocity is directly influenced by cadence, with higher PKAR velocities noted when participants use higher cadences (Earhart & Horak, 2004). Participants did not hold onto anything during that period

of stepping. To assure that participants did not drift forward, backward, or side-to-side during stepping, I screwed a 0.15-m peg into the floor, and they stepped with their feet on either side of the peg, brushing against the peg with the feet from time to time (see Figure 1). During the 30-min period, I recorded the position of the participant in space by tracking reflective markers placed on the acromion processes bilaterally and at the inferior angle of the left scapula. The left scapula marker served to make the marker set asymmetrical so that the computer could clearly and consistently identify the left and right acromial markers. Markers affixed bilaterally over the second metatarsal head, posterior calcaneus, and lateral malleolus, and three stationary markers affixed to the floor were also recorded. Eight digital Hawk cameras (Motion Analysis Corp., Santa Rosa, CA) performed three-dimensional motion capture. The cameras were mounted in a circle on the ceiling such that each marker was always visible by at least three cameras. Data were collected at 100 Hz.

Immediately upon completion of the second session, I asked participants to give their subjective impressions of the two sessions and to state which of the two sessions, walking or running, required more exertion. Limb lengths were measured after completion of the experiment and on a separate day from either of the two experimental sessions. Participants stood in a comfortable position, and I used a measuring tape to determine their limb length from the floor to the greater trochanter of the right lower extremity.

Data Analysis

A 6-Hz second-order Butterworth filter filtered kinematic data. I then compared participants' linear walk-to-run transition speed on a standard treadmill with their angular walk-to-run transition speed on the circular treadmill by converting the angular speeds of the inner and outer feet (i.e., left and right feet) on the rotating disk to linear speeds and plotting those values versus the linear walk-to-run transition speed obtained experimentally. I compared values for linear versus circular treadmill transition speeds by using a one-way repeated measures analysis of variance (ANOVA; $p < .05$). The ANOVA enabled me to compare linear transition speed with both inner and outer limb speeds at transition on the circular treadmill in a single test. All participants were included in that analysis. I also calculated the correlations between limb length and transition speeds and between linear and circular treadmill transition speeds.

During the 30-min period of stepping in place following treadmill stimulation, all participants demonstrated PKAR and inadvertently turned in circles. I calculated each participant's angular velocity across that 30-min period by taking the first derivative of the measured trunk position relative to space. Using EVaRT Version 4.4 motion analysis software (Motion Analysis Corp., Santa Rosa, CA), I analyzed trunk position, and I defined trunk position as the angle formed by a line drawn between the two acromion markers and two stationary floor markers. Angular velocity data versus time were plotted for the 30-min period, and I fitted those curves with the following two functions: (a) A two-parameter exponential rise to maximum function fitted to the first 2 min of the response yielded values for maximum velocity and decay time constant; and (b) a three-parameter exponential decay function fitted to the data from minutes 2 through 30 yielded values for initial velocity, asymptote, and decay time constant. I compared values for each of the curve-fit parameters between the walk and run conditions by using paired t tests ($p < .05$). Those analyses included only 9 participants because 1 participant demonstrated a very long-lasting PKAR in both the walk and run sessions. In fact, she showed no decay in PKAR velocity across the entire 30-min period of stepping in place, and her data as such could not be fitted effectively with the exponential decay function.

Results

Walk-to-Run Transition Velocities

Participants' self-selected walk-to-run transition speeds on the standard treadmill ranged from 1.9 to 2.6 m/s, averaging 2.2 ± 0.2 m/s. Participants' self-selected walk-to-run transition speeds on the circular treadmill ranged from 175 to 245 deg/s, averaging 204.9 ± 18.7 deg/s. The linear speed of the outer limb at transition on the circular treadmill ranged from 2.0 to 2.6 m/s, averaging 2.2 ± 0.2 m/s, and that of the inner limb ranged from 0.8 to 1.3 m/s, averaging 1.1 ± 0.2 m/s. Participants with higher transition speeds on the standard treadmill also had higher transition speeds on the circular treadmill. The correlation between transition speeds for the standard versus the circular treadmill was .90 ($p < .01$). Figure 2 shows transition speed on the circular treadmill versus transition speed on the standard treadmill, plotted for the outer (black circles) and inner (gray circles) limbs, respectively. The black line denotes where the data would fall if outer limb speed on the circular treadmill perfectly matched the standard treadmill transition speed. The gray line denotes where the data would fall if inner limb speed on the circular treadmill perfectly matched the standard treadmill transition speed. Actual data fell along the black line, indicating that transition speed on the standard treadmill was very similar to the linear speed of the outer limb at transition on the circular treadmill. There was no significant difference between the standard treadmill transition speed and the speed of the outer limb at transition on the circular treadmill. However, the speed of the inner limb at transition on the circular treadmill was significantly lower than were (a) the transition speed on the standard treadmill and (b) the outer limb speed at transition. All participants perceived the running session as requiring less exertion than the walking session did.

Figure 3 shows the relationship of limb length to transition speed on the standard and circular treadmills (outer limb only). The correlation between limb length and transition speed was weak ($r = .12$, $p = .74$, between limb length and standard transition speed; $r = .16$, $p = .66$, between limb length and circular transition speed).

PKAR

Regardless of whether participants walked or ran on the treadmill, all demonstrated PKAR following 15 min of treadmill exposure. Figure 4 shows representative PKAR responses from a single participant following running (A) and walking (B) on the circular treadmill. That participant showed a slightly higher velocity for postrun than for postwalk PKAR. Other participants showed the opposite relationship; their postwalk PKAR velocity was slightly greater than was their postrun PKAR velocity. The average postrun (C) and postwalk (D) PKAR responses across all 9 participants whose PKAR responses could be adequately fitted with an exponential decay function are also shown in Figure 4. Note the similarity of the curve-fit values for those averaged graphs.

There were no significant differences in initial velocity, asymptote level, decay time constant, or goodness of curve fit for the exponential decay functions fitted to the postrun and postwalk conditions (paired t tests, $p < .05$). Figure 4 shows equations of the form $y = y_0 + ae^{-bx}$ where y_0 is the asymptote level, a is initial velocity, and $1/b$ is the decay time constant for each curve. Average values for each of those parameters are provided in Table 1. Curve fits for minutes 0–2, which were fitted with an exponential rise to maximum function, were quite poor, with average R^2 values $.080 \pm .10$ for the postrun condition and $.17 \pm .21$ for the postwalk condition. Given those poor curve fits, values for maximum velocity and rise time constant could not be obtained. Those findings contrast with results of previous studies of PKAR; in those studies, data from minutes 0–2 were successfully fitted with a rise to maximum function. Data obtained in this study indicated a much more rapid rise in PKAR velocity at the outset of the response in both the postrun and postwalk conditions than has been observed previously. Because curve

fits were not possible for those data, I base that statement on visual observation of the PKAR plots in the present study as compared with those presented in former work. The present plots reached peak velocity at approximately 30 s, whereas peak velocity was typically reached at approximately 2 min in former studies.

Discussion

What Factors Contribute to Walk-to-Run Transition Speed?

For all participants, the self-selected walk-to-run transition speed on the standard treadmill matched very closely the speed of the outer limb at the self-selected walk-to-run transition speed on the circular treadmill. Given that relationship, it appears likely that transition speed was not determined by inner limb factors but rather was influenced primarily by the outer limb. By comparing what may be similar or different between the outer limb when participants locomote on the circular treadmill and both limbs when participants locomote on a standard treadmill, one can gain insights into which factors proposed in the literature to determine transition speed are likely to actually be playing a role. In the following paragraphs, I consider the various hypotheses that have been put forth in light of this new evidence from the circular treadmill.

According to one hypothesis, the walk-to-run transition may be made when it is energetically most efficient to switch gait patterns. That has been shown not to be the case on a standard treadmill; participants clearly transitioned from a walk to a run before it was metabolically optimal (Brisswalter & Mottet, 1996; Hreljac, 1993; Tseh et al., 2002). Those participants, however, consistently reported that running was easier than walking at the transition speed (Hreljac). Participants in the present study chose similar speeds for transition on the standard and circular treadmills and unanimously reported that running was easier than walking at the transition speed. That finding may suggest that the walk-to-run transition on the circular treadmill, like that on the standard treadmill, is made before it is energetically optimal to do so. That suggestion is purely speculative, however, given that no metabolic measures were determined in the present study.

According to another hypothesis, transition speed is determined in part by limb length because limb length limits the maximum spread of the lower limbs (Thorstensson & Roberthson, 1987). Minetti et al. (1994) proposed that upon approaching the limit of stride length, one must increase stride frequency to further increase locomotor speed, and that the increase in stride frequency may, in turn, increase internal work. They suggested that switching to a run may decrease internal work despite the higher stride frequency in running than in walking. Recent investigators have questioned the limb length hypothesis, however, noting that limb length is a poor predictor of transition speed (Hanna et al., 2000; Raynor et al., 2002). Our data support the latter studies, arguing against the hypothesis that stride length (or limb length) determines walk-to-run transition speed. The correlation between transition speed and limb length was quite low. Note that the relationship reported by Thorstensson and Roberthson was also not very strong and that their study sample included a wider range of limb lengths. Also, because of the small diameter of the circular treadmill and its curvature, participants are not physically able to take strides that are as long as those used during walking on a standard treadmill or over ground. Thus, participants were never pushed to the limits of stride length while on the circular treadmill. Despite that fact, their walk-to-run transition speeds on the circular treadmill (calculated for the outer limb) were quite similar to their walk-to-run transition speeds on the standard treadmill. That finding suggests that maximum stride length, as determined by limb length, is not a critical factor in driving the walk-to-run transition, at least on the circular treadmill. The effect of walking or running at different radii from the center of the circular treadmill should be examined in future studies. I was unable to assess how that variable might influence transition speed because the treadmill used in this study had a walking area of only

52 cm on the perimeter, leaving little room for changes in radial position during treadmill locomotion.

On the basis of the present observations, I conclude that limb length (and, subsequently, maximum stride length) may not be the major determinant of walk-to-run transition speed. Rather, the similarity of the outer limb's speed on the circular treadmill at transition and the speed of transition on the standard treadmill lends support to previous suggestions that muscular factors may play a large role in determining transition speed. That suggestion assumes that the same movement patterns are being used on the linear and circular treadmills. Perhaps the transition functions to prevent tibialis anterior overexertion that may occur beyond a given speed, as suggested by Hreljac (1995) and by Prilutsky and Gregor (2001). Alternatively, or perhaps in addition, the force-length-velocity properties of the soleus may contribute to the determination of transition speed as suggested by Neptune and Sasaki (2005). On the basis of my observations, I also cannot eliminate a possible contribution of loading rate (Raynor et al., 2002) or inverted pendulum dynamics (Kram et al., 1997). Whatever the mechanism, it appears to be similar for transitions on the circular and standard treadmills, indicating a common mechanism for adapting to increasing speed of locomotion on two very different moving surfaces.

Implications of Postrun PKAR

All participants demonstrated PKAR following both running and walking. That finding indicates that podokinetic stimulation influences forms of locomotion other than those used on the circular treadmill (e.g., participants demonstrated PKAR during walking in place even in sessions in which they did not walk on the treadmill but instead ran). That observation suggests that the podokinetic system controls the general locomotor trajectory. That notion is in keeping with previous results showing that PKAR transfers from forward to backward walking (Earhart et al., 2001) and from stepping to hopping (Earhart et al., 2002a). The results of the aforementioned body of work indicate that PKAR is an adaptive response because it can be acquired, retained, and transferred—the three hallmark features of adaptation (Schmid & Jeannerod, 1985).

PKAR following running was quite similar to that following walking with regard to initial velocity, asymptote level, and decay time constant. That finding indicates that similar adaptive responses occurred regardless of whether the participant walked or ran on the treadmill. As such, it is apparent that one does not need periods of double support while locomoting on the rotating surface to induce adaptation. That result is consistent with the observation that, for a given treadmill speed, changes in cadence during locomotion on the rotating treadmill, and therefore changes in amount of time spent with the feet on the ground, do not alter PKAR responses (Earhart & Horak, 2004). The present results also suggest that common mechanisms for control of locomotor trajectory are at work for both walking and running. That view is in keeping with the results of Li et al. (1999), who demonstrated similar coordinative strategies for walking and running at transition speed.

Comparison of Present Results With Those of Former PKAR Studies

The PKAR responses observed in this study differed from those of previous studies. Rise of velocity in the initial minutes of the response was much more rapid in the present study than it was in former work. Because of differences in method, it is difficult to compare the present study directly with former studies to determine why the present results differed. This is the first study in which a researcher examined PKAR following locomotion on such a rapidly rotating treadmill. Velocities used in this study ranged from 175 to 245 deg/s, whereas the maximum velocity examined previously was 90 deg/s (Weber et al., 1998). Moreover, walking or running at that high speed was a challenging task, and participants' performance was not as

fluid as it was at lower velocities. As such, participants likely experienced higher vertical ground reaction forces on each foot contact with the surface in the present study than did participants in previous work, and the high forces may have resulted in altered vestibular stimulation. The repeated vestibular stimulation with each foot contact during circular treadmill locomotion may have resulted in altered vestibular–podokinetic interactions during the initial portion of PKAR, given the known importance of vestibular influences on PKAR rise (Earhart et al., 2004). However, vestibular influence on later portions of PKAR is known to be minimal. The minimal vestibular influence may account for the absence of differences between PKAR following walking and running despite the fact that vertical ground reaction forces were higher for running than for walking at a given speed (Li & Hamill, 2002). Further study is needed to determine whether the differences noted in this study are related to the duration of treadmill locomotion, high treadmill velocity, altered vestibular stimulation with jarring foot impacts, or to other factors, alone or in combination.

Summary

The results of the present work show a clear relationship between walk-to-run transition speeds on a rotating circular treadmill and walk-to-run transition speeds on a standard linear treadmill, suggesting that similar mechanisms may be at work in controlling walk-to-run transitions on the two different moving surfaces. They further show strikingly similar adaptive locomotor aftereffects following walking or running on the circular treadmill, suggesting similar mechanisms of adaptive control of locomotor trajectory for walking and running. Taken together, the results suggest that walk-to-run transitions and locomotor trajectory during walking and running are governed by general control mechanisms that are not specific to the direction of locomotion (angular or linear) or to the form of locomotion being used.

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FIGURE 1. Illustration of experimental setup for (left) walking and running sessions and (right) for podokinetic after-rotation (PKAR).

FIGURE 2.

Plot of each participant's self-selected walk–run transition speed on a standard treadmill versus the speed of his outer and inner limbs at his self-selected transition speed on the circular treadmill. Note that outer limb speed at walk–run transition on the circular treadmill was very similar to the walk–run transition speed on the standard treadmill, whereas inner limb speed was much lower.

FIGURE 3.

Plot of each participant's limb length versus his or her transition speed on the standard treadmill (open squares) and his or her outer limb speed at transition on the circular treadmill (filled circles). The relationship between limb length and transition speed was weak for the standard and the circular treadmills.

FIGURE 4.

Representative postrun (A) and postwalk (B) podokinetic after-rotation (PKAR) responses in a single participant and average curves across all participants for postrun (C) and postwalk (D) PKAR. All plots were fitted with an exponential decay curve described by the equation $y = y_0 + ae^{-bx}$. Note the similar velocities and profiles of the average curves. There were no significant differences between postrun PKAR and postwalk PKAR.

TABLE 1
Podokinetic After-Rotation (PKAR) Curve-Fit Values

Variable	Postrun PKAR		Postwalk PKAR	
	<i>M</i>	<i>SD</i>	<i>M</i>	<i>SD</i>
Initial velocity (deg/s)	10.18	3.96	9.11	5.33
Asymptote velocity (deg/s)	0.08	1.83	0.02	1.70
Decay time constant (min)	5.44	2.52	5.87	2.28
Goodness of curve fit (R^2)	.64	.23	.74	.12

Note. *SD* = Standard deviation