Explicit control of step timing during split-belt walking reveals interdependent recalibration of movements in space and time

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ABSTRACT

Split-belt treadmills that move the legs at different speeds are thought to update internal representations of the environment, such that this novel condition generates a new locomotor pattern with distinct spatio-temporal features to those of regular walking. It is unclear the degree to which such recalibration of movements in the spatial and temporal domains is interdependent. In this study, we explicitly altered the adaptation of limb motions in either space or time during split-belt walking to determine its impact on the other domain. Interestingly, we observed that motor adaptation in the spatial domain was susceptible to altering the temporal domain, whereas motor adaptation in the temporal domain was resilient to modifying the spatial domain. This nonreciprocal relation suggests a hierarchical organization such that the control of timing in locomotion has an effect on the control of limb position. This is of translational interest because clinical populations often have a greater deficit in one domain compared to the other. Our results suggest that explicit changes to temporal deficits cannot occur without modifying the spatial control of the limb.

Keywords: locomotion, motor learning, split-belt, spatio-temporal, sensorimotor adaptation, kinematics

1 INTRODUCTION

We are constantly adapting our movements to demands imposed by changes in the environment or our body. In walking, this requires the adaptation of spatial and temporal gait features to control ”where” and ”when” we step, respectively. Particularly, in split-belt walking when one leg moves faster than the other, it has been observed that subjects minimize spatial and temporal asymmetries by adopting motor patterns specific to the split environment(Malone et al., 2012; Iturralde and Torres-Oviedo, 2019). It is thought that this is achieved by updating internal representations of the treadmill for the control of the limb in space and time(Malone et al., 2012). There is a clinical interest in understanding the interdependence in the control of these two aspects of movement because pathological gait often has a greater deficiency in one domain compared to the other (Finley et al., 2015; Malone and Bastian, 2014). Thus, there is a translational interest to determine if spatial and temporal asymmetries in clinical populations can be targeted and treated independently.

Ample evidence supports that the adaptation, and hence control, of spatial and temporal gait features is dissociable. Notably, studies have shown that inter-limb measures such as step timing (temporal) and step position (spatial) adapt at different rates (Sombric et al., 2017; Malone and Bastian, 2010), they exhibit different generalization patterns (Torres-Oviedo and Bastian, 2010), and follow distinct adaptation dynamics throughout development (Vasudevan et al., 2011; Patrick et al., 2014) or healthy aging (Sombric et al., 2017). In addition, several behavioral studies have shown that the adaptation of spatial measures can be altered (Malone and Bastian, 2010; Malone et al., 2012; Long et al., 2016) without modifying the adaptation of temporal gait features. However, the opposite has not been demonstrated. For example, altering intra-limb measures (i.e., characterizing single leg motion) of timing such as stance time duration (Afzal et al., 2015; Krishnan et al., 2016) also leads to changes in intra-limb spatial features such as stride lengths. In sum, the spatial and temporal control of the limb is thought to be dissociable, but it remains unclear if the adaptation of internal representations of timing can be altered and what is the impact of such manipulation in the temporal domain on the spatial control of the limb.

In this study we aimed to determine the interdependence between the spatial and temporal control of the limbs during walking, particularly of inter-limb parameters characterizing bipedal coordination. We hypothesized that spatial and temporal inter-limb features are controlled independently based on previous studies demonstrating their dissociation. To test this hypothesis, subjects walked on a split-belt treadmill, which requires the adaptation of spatial and temporal gait features. We further altered the adaptation of one domain and observed the impact on the adaptation of the other domain.

2 MATERIAL AND METHODS

We recruited twenty-one healthy young subjects (13 women, 8 men, mean age 24.69 ± 4 years) to voluntarily participate in this study. Subjects were randomly assigned to three groups (n=7, each): 1) control, 2) temporal feedback, 3) spatial feedback to determine if altering the adaptation of limb motion on either the spatial or the temporal domain with visual feedback during split-belt walking had an impact on the adaptation of the other domain (Figure 1A). Notably, if the control of these two domains was dissociable, altering one would not have an effect on the other. Alternatively, if they were interdependent, modifying the adaptation of one domain not only would have an effect on the targeted domain, but will also alter the other one. The protocol was approved by the Institutional Review Board of the University of Pittsburgh and all subjects gave informed consent prior to testing.

2.1 Experimental Protocol

All subjects walked on a split-belt treadmill during four experimental phases: Baseline, Familiarization, Adaptation, and Post-adaptation. The speed for each belt during these phases is shown in Figure 1B. This speed profile enabled individuals to walked at an averaged speed of 0.75 m/s throughout the experiment. In the Baseline phase, individuals walked with the two belts moving at the same speed of 0.75 m/s for 150 strides ($\sim$ 3 min). Recordings from these phase were used as the reference gait for every individual. In the Familiarization phase, all participants also walked at 0.75 m/s for 150 strides, but only subjects in the feedback groups received the same visual feedback that they were going to experience during the subsequent Adaptation phase. This was done to allow feedback groups to become habituated to use the provided visual feedback to control either spatial (spatial feedback group) or temporal (temporal feedback group) gait features. In the Adaptation phase, the belts were moved at a 2:1 ratio (1:0.5 m/s) for 600 strides ($\sim$ 13 min). We selected these specific belt speeds because other studies have indicated that they induce robust sensorimotor adaptation (Reisman et al., 2005; Mawase et al., 2014; Sombric et al., 2017; Vervoort et al., 2019) and we observed in pilot tests that subjects with visual feedback at these speeds could successfully modify the spatial and temporal gait features of interest. The (self-reported) dominant leg walked on the fast belt. In the Post-adaptation phase, all individuals walked with both belts moving at 0.75 m/s for 450 strides ($\sim$ 10 min). This phase was used to quantify gait changes following the Adaptation phase. The treadmill's belts were stopped at the end of each experimental phase. A handrail was placed in front of the treadmill for safety purposes, but individuals did not hold it while walking. A custom-built divider was placed in the middle of the treadmill during the entire experimental protocol to prevent subjects from stepping on the same belt with both legs. Subjects also wore a safety harness (SoloStep, SD) that did not interfere with their walking (no body weight support).

We tested three groups: 1) control group, 2) temporal feedback group, 3) spatial feedback group. The control group was asked to "just walk" without any specific feedback on subjects' movements. Each subject in the temporal or spatial feedback groups was instructed to either maintain his/her averaged baseline step time (temporal feedback group) or averaged baseline step position (spatial feedback group) when the feedback was on. Step time was defined as the time period from foot landing of one leg to foot landing of the other leg (Figure 1C). Step position was defined as the sagittal distance between the leading leg's ankle to the hip at heel strike (Figure 1D). Panels C and D in Figure 1 show sample screen shots of the visual feedback observed by each group on a screen placed in front of them. More specifically, we permanently displayed either temporal or spatial targets (blue rectangles) indicating the averaged step time (temporal feedback group) or averaged step position (spatial feedback group) across legs during baseline walking. These targets turned green when subjects achieved the targeted baseline values and they turned red when they did not. A tolerance of $\pm 0.75\%$ and $\pm 1.25\%$ of the baseline value was given to subjects in the spatial and temporal feedback groups, respectively. Yellow lines indicated the actual step position and step time for each leg at every step. Thus, subjects could appreciate how far they were from the targeted spatial or temporal value at every step.

2.2 Data Collection

Kinetic and kinematic data were collected to quantify subjects' gait. Kinematic data was collected at 100 Hz with a motion capture system (VICON motion systems, Oxford, UK). Passive reflective markers were placed bilaterally on bony landmarks at the ankle (malleolus) and the hip (greater trochanter). Kinetic data was collected at 1000 Hz with the instrumented split-belt treadmill (Bertec, OH). The normal ground reaction force (F_z) was used to detect when the foot landed (i.e., heel strike) or was lifted off (i.e., toe off). A threshold of 10 N was used for detecting heel strikes and toe offs for data analysis, whereas a threshold of 30 N was used for counting strides in real-time.

2.3 Data Analysis

2.3.1 Gait parameters

We computed six gait parameters previously used (Malone et al., 2012) to quantify the adaptation of spatial and temporal control of the limb during split-belt walking: S_{out}, T_{out}, S_A, T_A, $S_{!A}$, and $T_{!A}$. We used S_{out} and T_{out} because our feedback was designed to directly alter these metrics. For example, subjects in the spatial feedback group were given feedback to maintain the same baseline step position in both legs. S_{out} is, therefore, a good metric of performance for the spatial feedback group since it quantifies the difference in step positions, α_f and α_s, when taking a step with the fast and slow leg, respectively. Formally expressed:

$$S_{out} = \frac{\alpha_f - \alpha_s}{\alpha_f + \alpha_s} \tag{1}$$

By convention, S_{out} is positive when the fast leg's foot lands farther away from the body when taking a step than the slow leg's one (i.e., $\alpha_f > \alpha_s$). S_{out} is zero during baseline and subjects in the feedback group were instructed to maintain this value during split-belt walking.

Similarly, subjects in the temporal feedback group were given feedback to maintain the same baseline step times in both legs. T_{out} is, therefore, a good metric of performance for the temporal feedback group since it quantifies the difference in step times, t_s and t_f. Formally expressed:

$$T_{out} = \frac{t_s - t_f}{t_s + t_f} = \frac{t_s - t_f}{T_{stride}} \tag{2}$$

Where T_{stride} is the stride time (i.e., time interval between two consecutive heel strikes with the same leg). By convention, T_{out} is positive when the slow leg's step time is longer that the fast leg's one. T_{out} is zero during baseline and subjects in the feedback group were instructed to maintain this value during split-belt walking. It has been previously shown that S_{out} and T_{out} are adapted during split-belt walking to minimize spatial and temporal baseline asymmetries defined as S_A and T_A, respectively (Malone et al., 2012). Therefore, we also quantified S_A and T_A because these are adaptive parameters (Malone et al., 2012; Reisman et al., 2005; Malone and Bastian, 2010) that could be indirectly altered by our spatial and temporal feedback even if subjects in these groups were not explicitly instructed to modify them.

S_A quantifies differences between the legs in where they oscillate with respect to the body. The oscillation of each leg was computed as the ratio between two distances: step position (α) and stride length (γ) (i.e., anterior-posterior distance from foot position at heel strike to ipsilateral foot position at toe off). Thus, S_A was computed as the difference between these ratios when taking a step with the slow leg (i.e., slow leg leading) vs. the fast leg (see Eq. 3).

$$S_A = \frac{\alpha_s}{\gamma_s} - \frac{\alpha_f}{\gamma_f} \tag{3}$$

In the temporal domain, T_A quantified the difference in double support times (i.e., period during which both legs are on the ground) when taking a step with the fast leg (DS_s) or slow leg (DS_f), respectively (see Eq. 4). In other words, DS_s is defined as the time from fast heel strike to slow toe off and DS_f as the time from slow heel strike to fast toe off.

$$T_A = DS_s - DS_f \tag{4}$$

Lastly, we computed gait parameters defined as $S_{!A}$ and $T_{!A}$, to test the specificity of our feedback. Namely, it has been previously observed that these parameters do not change as subjects walk in the split-belt environment (Malone et al., 2012; Reisman et al., 2005; Yokoyama et al., 2018). Thus, these measures are thought to simply reflect the speed difference between the legs, and hence, we expected that our feedback would not alter them. Specifically, $S_{!A}$ quantifies the difference between the fast and slow leg's ranges of motion γ_f and γ_s during their respective stance phase, which is defined as the interval when the foot is in contact with the ground. Formally expressed as:

$$S_{!A} = \frac{\gamma_f - \gamma_s}{\gamma_f + \gamma_s} \tag{5}$$

The non-adaptive measure in the temporal domain $T_{!A}$ quantifies the difference between the slow and fast leg's stance time durations, which we labeled as ST_s and ST_f, respectively. Formally expressed as:

$$T_{!A} = \frac{ST_s - ST_f}{T_{stride}} \tag{6}$$

2.3.2 Outcome measures

We computed *steady state* and *after-effects* to respectively characterize the adaptation and recalibration of walking in the spatial and temporal domains. Both of these outcome measures were computed for each gait parameter described in the previous section. *Steady state* was used to characterize the spatial and temporal features of the adapted motor pattern once subjects reached a plateau during split-belt walking. *Steady state* was computed as the averaged of the last 45 strides during the Adaptation phase, except for the very last 5 strides to exclude transient steps when subjects were told to hold on to the handrail prior to stopping the treadmill. *After-effects* were used to characterize the recalibration of subjects' internal representation of the environment (Roemmich and Bastian, 2015) leading to gait changes that were sustained following split-belt walking compared to baseline spatial and temporal gait features. *After-effects* were computed as the averaged value for each gait parameter over the first thirty strides of post-adaptation. We used 30 strides, rather than only the initial 1 to 5 strides, because we were interested in characterizing long lasting after-effects (Long et al., 2015; Mawase et al., 2017; Roemmich and Bastian, 2015). We removed baseline biases from both measures by subtracting the baseline values for each gait parameter averaged over the last 45 strides during baseline (minus the very last transient 5 strides). This was done to exclude individual biases before aggregating subjects' outcome measures in every group.

2.4 Statistical analysis

We were interested to determine if altering the adaptation of limb motion on either the spatial or the temporal domain with visual feedback during split-belt walking had an impact on the adaptation and recalibration of gait features in the other domain. Thus, we performed separate analysis contrasting outcome measures of the control (reference) group to either the spatial feedback group or the temporal feedback group. More specifically, we used separate two-way repeated measures ANOVAs to identify effects of either spatial or temporal feedback on gait features within the same domain (e.g., $T \rightarrow T$) or the other domain (e.g., $T \rightarrow S$). For example, we did a two-way repeated measures ANOVA to test the effect of group (i.e., spatial feedback vs. control) and domain specificity (i.e., domain-specific vs. not domain-specific) on the *steady state* of adaptive parameters T_A and S_A. If a significant group effect or group by domain interaction was found ($p < 0.05$), we used Fisher's LSD *post-hoc* testing to assess if main effects were driven by differences between the feedback group and reference group in either domain. We applied a Bonferroni correction to account for multiple comparisons in the *post-hoc* analysis, resulting in a significance level set to $\alpha = 0.025$. Lastly, we performed independent sample t-tests to determine if *after-effects* were significantly different from baseline since all statistical analyses were done with unbiased data (i.e., baseline bias removed). A significance level was also set to $\alpha = 0.025$ to account for multiple comparisons. We used Stata (StataCorp LP, College Station, TX) for all statistical analyses.

3 RESULTS

Confirmation of results supporting dissociable representation of spatial and temporal walking features.

Spatial and temporal gait features adapted and recalibrated independently when feedback was used to alter the spatial control of the limb. This is indicated by the qualitative group differences between the time courses of S_{out} during adaptation and post-adaptation (top panels in Figure 2A and 2B, respectively) contrasting the overlapping time courses of T_{out} in the control group (red trace) and spatial feedback group (blue trace) (bottom panels in Figures 2A and 2B). Accordingly, we found a significant group effect ($p = 0.0047$) and group by domain interaction ($p = 0.0094$) on the steady states of S_{out} and T_{out}. *Post-hoc* analysis indicated that the spatial feedback only reduced the steady state of S_{out}, ($S \rightarrow S : p = 0.0002$), but not the steady state of T_{out} ($S \rightarrow T : p = 0.3896$). The dissociation between spatial and temporal control was also shown by the after-effects of S_{out} and T_{out} in the control vs. spatial feedback groups. Notably, we found a significant group effect ($p = 0.0350$) and group by domain interaction ($p = 0.0418$) indicating a distinct effect of spatial feedback on the recalibration of T_{out} and S_{out}. While both groups had after-effects different from zero (control group: $p = 0.0003$; spatial feedback group: $p = 0.0164$), the spatial feedback reduced the after-effects of S_{out} compared to the control group ($S \rightarrow S : p = 0.0031$). In contrast, spatial feedback did not change the after-effects of T_{out} ($p = 0.9042$). In sum, spatial feedback had a domain-specific effect: it altered the adaptation and recalibration of step position (targeted spatial parameter) without modifying the adaptation and aftereffects of step time (T_{out}).

The dissociation in adaptation and recalibration of spatial and temporal representations of walking was also supported by the analysis of spatial and temporal features known to be adapted by the split-belt task, but not directly targeted by our feedback. Namely, the spatial feedback also modified the adaptation and post-adaptation time courses of the symmetry in legs' oscillation, quantified by S_A, which is expected given its relation to step position. Note that the time courses of S_A for the spatial feedback group (blue trace) and control group (red trace) do not overlap during adaptation and post-adaptation (top panel Figure 3A and 3B). In contrast, the time courses of double support asymmetry (T_A) were not altered by the spatial feedback, as shown by the overlap of T_A values during adaptation and post-adaptation of the temporal feedback and control groups (bottom panel Figure 3A and 3B). Consistently, we found a significant group by domain interaction in the T_A's and S_A's steady states ($p = 0.0189$) and a significant group effect in the T_A's and S_A's after-effects ($p = 0.0008$). *Post-hoc* analyses revealed that these effects were driven by group differences in S_A's steady state ($S \rightarrow S_A : p = 0.0033$) and S_A's after-effects ($S \rightarrow S_A : p = 0.0045$), rather than group differences in T_A's steady state ($S \rightarrow T_A : p = 0.727$) and T_A's after-effects ($T \rightarrow T_A : p = 0.6341$). Thus, after-effects in S_A and T_A were significantly different from zero in all groups (control group: $T_A p = 0.0044$ and $S_A p = 0.0009$; spatial feedback group: $T_A p = 0.0007$ and $S_A p = 0.0542$), but only those of S_A were reduced in the spatial feedback group compared to controls. These results reiterated that changes in the spatial domain did not modify the temporal control of the limb in the temporal domain, replicating previous findings (Malone et al., 2012; Long et al., 2016).

New evidence for interdependent representations of spatial and temporal walking features.

Interestingly, we found that spatial and temporal gait features were not independent in their adaptation and recalibration when feedback was used to alter the temporal control of the limb. This is indicated by the qualitative differences between the time courses of T_{out} and S_{out} during the adaptation (Figure 4A) and post-adaptation phases (Figure 4B). Namely, the control group (red traces) and temporal feedback group (yellow traces) are different in both spatial and temporal parameters. Consistently, we found a significant group effect on steady states of S_{out} and T_{out} ($p = 0.0001$), highlighted by the black rectangles in Figure 4A. While the temporal feedback group was designed to alter step times, and hence significantly reduce T_{out} ($T \rightarrow T : p = 0.0075$), we did not anticipate a reduction in the adaptation of S_{out} ($T \rightarrow S : p = 0.0003$) because this parameter was not directly targeted. The interdependence between spatial and temporal domains was also shown by the analysis of aftereffects in post-adaptation (Figure 4B). Notably, we found a significant group ($p = 0.0008$) and group by domain interaction ($p = 0.0128$). *Post-hoc* analyses indicated that temporal feedback did not change the recalibration of T_{out} ($T \rightarrow T : p = 0.673$), but altered the recalibration of S_{out} ($T \rightarrow S : p < 0.0001$). The non-significant effect on the recalibration of T_{out} was expected given that aftereffects in this parameter are very short lived resulting in T_{out} after-effect values that are non-significantly different from zero (control group: $p = 0.4322$; temporal feedback group: $p = 0.8550$). In contrast, both groups had after-effects in S_{out} that were significantly different from zero (control group: $p = 0.0003$; temporal feedback group: $p = 0.0021$); but they were unexpectedly smaller in the temporal feedback group compared to the control group. In sum, the temporal feedback impact on adaptation and recalibration of S_{out} (spatial parameter) indicated an interdependence between the spatial and temporal control of the limb.

The possible interdependence in space and time was further supported by the analysis of spatial and temporal features known to be adapted by the split-belt task, but not directly targeted by our feedback. Namely, the temporal feedback also modified the adaptation and post-adaptation time courses of the symmetry in legs' oscillation, quantified by S_A, which is a spatial measure related to step position. Note that the time courses of S_A for the temporal feedback group (yellow trace) and control group (red trace) do not overlap during adaptation and post-adaptation (bottom panel Figure 5A and 5B). In contrast, the time courses of double support asymmetry (T_A) were not altered by the temporal feedback, as shown by the overlap of T_A values during adaptation and post-adaptation of the temporal feedback and control groups (top panel Figure 5A and 5B). Consistently, we found a group effect in the T_A's and S_A's steady states ($p = 0.0382$) and after-effects ($p = 0.0050$). *Post-hoc* analyses revealed that these effects were driven by group differences in S_A's steady state ($T \rightarrow S_A : p = 0.0053$) and S_A's after-effects ($T \rightarrow S_A : p = 0.0007$), rather than group differences in T_A's steady state ($T \rightarrow T_A : p = 0.6953$) and T_A's after-effects ($T \rightarrow T_A : p = 0.7784$), which we expected given the relation between T_A and the temporal measure (T) directly altered with the temporal feedback. Thus, after-effects in S_A and T_A were significantly different from zero in all groups (control group: $T_A p = 0.0044$ and $S_A p = 0.0009$; temporal feedback group: $T_A p = 0.0009$ and $S_A p = 0.008$), but only those of S_A were reduced in the temporal feedback group compared to controls. In sum, these results indicate that temporal feedback did not have a ubiquitous effect in all gait parameters, but it did alter the adaptation and recalibration of the legs' oscillation, which also characterizes the spatial control of the limb in locomotion.

Temporal feedback modified the split-belt task to a greater extent than the spatial feedback.

Surprisingly, temporal feedback altered the difference in stance times between the legs ($T_{!A}$), whereas the spatial feedback did not. This was unexpected given previous literature indicating that $S_{!A}$ and $T_{!A}$ do not change as subjects walk in the split-belt environment (Malone et al., 2012; Reisman et al., 2005; Yokoyama et al., 2018). Thus, we anticipated that either type of feedback (spatial or temporal) would not alter these ”non-adaptive” gait features. Qualitatively, we observed that this was the case for the spatial ($S_{!A}$), but not for the temporal ($T_{!A}$) “non-adaptive” parameter (Figure 6A). Note that $T_{!A}$ has a different time course for the control group (red trace) and the temporal feedback group (yellow trace), whereas $S_{!A}$ has the same time course for both groups. Consistently, we found a significant group effect ($p = 0.0010$) and group by domain interaction ($p = 0.01$). *Post-hoc* analysis revealed that the temporal feedback group reached a significantly lower steady state when compared to the control group ($T \rightarrow T_{!A} : p < 0.0001$), which contrasted the non-significant differences between the groups in steady state values of $S_{!A}$ ($T \rightarrow S_{!A} : p = 0.9878$). Conversely, the spatial feedback group exhibited the non-adaptive behavior of these parameters $S_{!A}$ and $T_{!A}$ that we anticipated. Namely, the time courses of $S_{!A}$ (Figure 6B, top panel) and $T_{!A}$ (Figure 6B, bottom panel) were overlapping in these two groups. This similarity is substantiated by the non-significant group ($p = 0.7835$) or group by domain interaction ($p = 0.3462$) on the steady states of these non-adaptive measures. In sum, feedback modifying the adaptation of spatial and temporal gait features had a distinct effect on 'non-adaptive" temporal parameters thought to only depend on the speed difference between the legs in the split-belt task.

4 DISCUSSION

4.1 Summary

Our study confirms previous results suggesting that there are internal representations of space and time for predictive control of movement. We replicated previous results showing that altering the recalibration in the spatial domain does not impact the temporal domain. However, we also observed that the opposite was not true. That is, explicitly reducing the recalibration in the temporal domain altered movement control in space, suggesting some level of interdependence between these two domains. Interestingly, double support asymmetry was consistently corrected across the distinct spatio-temporal perturbations that subjects experienced, whereas spatial asymmetries were not. This indicates that correcting asymmetries in space and time is prioritized differently by the motor system. Our results are of translational interest because clinical populations often have greater deficits in either the spatial or the temporal control of the limb and our findings suggest that they may not be treated in isolation.

4.2 Separate representations for predictive control of movements in space and time

We find that adaptation of movements to a novel walking situation results in the recalibration of internal representations for predictive control of locomotion; which are expressed as robust after-effects in temporal and spatial movement features. This is consistent with the idea that the motor system forms internal representations of space (Marigold and Drew, 2017) and time (Avraham et al., 2017; Breska and Ivry, 2018; Drew and Marigold, 2015) for predictive motor control. Several behavioral studies suggest separate recalibration of these internal representations of space and time in locomotion because spatial and timing measures exhibit different adaptation rates in the mature motor system (Malone and Bastian, 2010; Darmohray et al., 2019) throughout development (Vasudevan et al., 2011; Patrick et al., 2014) or healthy aging (Sombric et al., 2017). Spatial and temporal recalibration also have distinct generalization patterns across walking environments (Torres-Oviedo and Bastian, 2010; Mariscal et al., 2018) and most importantly, altering the adaptation of spatial features does not modify the adaptation and recalibration of temporal ones, as shown by us and others (Malone et al., 2012; Long et al., 2016). This idea of separate representations of space and time in locomotion is also supported by clinical and neurophysiological studies indicating that different neural structures might contribute to the control (Rybak et al., 2006; Lafreniere-Roula and McCrea, 2005) and adaptation (Vasudevan et al., 2011; Choi et al., 2009; Statton et al., 2018) of the spatial and temporal control of the limb in locomotion.

4.3 Hierarchic control of timing leads to interdependent adaptation of movements in space and time

Nonetheless, we also found that explicit control of step timing modifies the adaptation and recalibration of movements in space. This result directly contradicts the dissociable adaptation of spatial and temporal features upon explicitly modifying the adaptation of step position (spatial parameter) (Malone et al., 2012; Long et al., 2016). We find two possible explanations to reconcile these findings. First, there might be a hierarchical relationship between the spatial and temporal control of the limb, such that timing cannot be manipulated without obstructing the adaptation of spatial features. This type of hierarchical organization is supported by a recent study indicating that lesions to interpose cerebellar nuclei altering the adaptation of double support (temporal parameter) also reduced the after-effects of spatial features (Darmohray et al., 2019), whereas the recalibration of spatial features can be halted without modifying the temporal ones (Darmohray et al., 2019). This type of hierarchical organization suggests that the execution of spatial and temporal control of the limb can be encoded by separate interneuronal networks (Rybak et al., 2006; Lafreniere-Roula and McCrea, 2005), but the volitional recruitment of those networks cannot occur in isolation. Second, it is possible that the observed interdependence arose as a byproduct of how we tested it. Namely, subjects had two possible strategies to maintain equal step times in the asymmetric split environment: 1) decrease the difference between step positions or 2) increase the difference between swing speeds. The latter strategy was probably less likely given human tendencies to self-select energetically optimal walking patterns (Margaria, 1976; Alexander, 1989; Bertram and Ruina, 2001). Notably, individuals naturally exploit passive dynamics to swing the legs (Perry, 1992a). Thus, increasing swing speed would have altered dramatically the metabolic cost associated to this phase of the gait cycle (Gottschall and Kram, 2005; Marsh et al., 2004; Umberger, 2010). In the same vain, we inadvertently reduce the stance time asymmetry associated to split-belt walking with the temporal feedback task. The stance time asymmetry is thought to be a key component for the spatio-temporal adaptation of walking induced by split-belt walking (Reisman et al., 2005). Therefore, subjects in the temporal feedback group might have reduced the adaptation of spatial parameters because the ”teaching” signal to update them was reduced. In sum, it remains an open question the extent to which temporal gait parameters, such as double support, can be explicitly modulated without altering the spatial control of the limb.

4.4 Relevance of double support symmetry over spatial asymmetries

We demonstrated that double support symmetry (i.e., T_A) is recovered in all groups, regardless of the task. This is in accordance with multiple observations that individuals consistently reduce double support asymmetries induced by split-belt walking since very early age (Patrick et al., 2014) or after lesions to cerebral (Reisman et al., 2007) or cerebellar regions (Vasudevan et al., 2011). Only children with hemispherectomies, where half of the cerebrum is missing, do not correct double support asymmetry when this is augmented (Choi et al., 2009). The adaptation and after-effects of double support were surprising to us because previous work showed that halting the adaptation of step position ($S_{out} \approx 0$) limited the correction of spatial errors (defined as S_a) (Malone et al., 2012). In an analogous manner, we anticipated that preventing the adaptation of step times ($T_{out} \approx 0$) during split-belt walking was going to limit the adaptation of double support asymmetry (i.e., temporal error (Malone et al., 2012)). However, we observed that individuals prioritize differently the correction of spatial and temporal asymmetries: they minimize temporal asymmetries, but not spatial ones. This might be because double support time is the transition period when the body mass is transferred from one leg to the other, which is demanding in terms of energy expenditure (Perry, 1992b). Therefore, double support symmetry might be critical for efficient body transfer between the limbs (Kuo et al., 2005; Ruina et al., 2005). Taken together our results suggests that the motor system prioritizes the maintenance of double support symmetry, which might be critical for balance control in bipedal locomotion.

4.5 Study implications

We provide a novel approach for manipulating stance time, which is a major deficit in stroke survivors (Patterson et al., 2008). It would be interesting to determine if this type of feedback overground or on a regular treadmill could lead to gait improvements post-stroke as those induced by split-belt walking (Reisman et al., 2013; Lewek et al., 2018). Our results also indicate that manipulating the adaptation of movements in the temporal domain alters movements in the spatial domain, suggesting that spatial and temporal deficits in individuals with cortical lesions (Finley et al., 2015; Malone and Bastian, 2014) cannot be treated in complete isolation. Only the correction of timing asymmetries through error-based sensorimotor adaptation could occur while preventing the adaptation of spatial ones, as we did in the spatial feedback group. However, the opposite is not possible, at least with the temporal feedback task that we used.

CONFLICT OF INTEREST STATEMENT

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

AUTHOR CONTRIBUTIONS

M.G. and N.V. equally contributed to data acquisition and processing. They also contributed in the interpretation of the data and final approval of the version to be published, and agreement to be accountable for all aspects of the work. G.T. contributions include conception and design of the work, analysis of the data, writing a complete draft of the manuscript, revising work for important intellectual content, final approval of the version to be published, and agreement to be accountable for all aspects of the work.

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FIGURE CAPTIONS

Figure 1: Expected outcomes, Paradigm and Feedback Visualization. **(A)** Expected outcomes for dissociable and interdependent internal representations of space and time. If dissociable, the feedback manipulation will only affect the targeted domain without changing the other domain. For example, spatial feedback (indicated with blue outline) would alter spatial features (S) of the motor pattern while temporal ones (T) remain invariant. On the other hand, if the domains are interdependent, feedback manipulation of one domain will also alter the other domain. For example, spatial feedback modifying spatial features of the motor pattern would also change temporal ones. **(B)** Split-belt walking paradigm used in all groups. Dashed lines separate the different experimental phases. All groups experienced the same number of strides during each phase (Baseline: 150, Familiarization: 150, Adaptation: 600, and Post-adaptation: 450). The two belts moved at the same speed ($0.75m/s$) during the Baseline and Familiarization phases. Only subjects in the feedback groups walked while observing their movements on a TV screen placed directly in front of them (Feedback On) during the familiarization phase. The feedback to these groups was also given during the Adaptation phase (gray shaded area) during which one belt (fast belt) moved at $1m/s$ and the other one (slow belt) moved at $0.5m/s$. Finally, during Post-adaptation subjects walked again with the two belts moving at the same speed ($0.75m/s$). **(C-D)** Visual feedback schematic. Schematic of the legs in the top row illustrate the step position (e.g., α_f and α_s) and step time (e.g., t_s), which were the walking features used in the spatial and temporal feedback tasks, respectively. Bottom rows in panel C and D illustrate the screen shots observed by individuals in the spatial feedback group (Panel C) or in the temporal feedback group (Panel D). Blue rectangles indicated the target step position or step time value that subjects had to achieve with each leg. These rectangles turned green when subjects met the desired step position or step time values and red when they did not. Yellow lines indicated either the step position value (Panel C) or the step time value (Panel D) at heel strike (HS) when taking a step with the right or left leg (e.g., left leg's

step position is shown in the screen shot #1). In the example shown, the step position was correct for the right leg but not for the left leg. The light grey progression bars showed in real-time either the the distance from the ankle to the hip markers as subjects swing the leg forward (Panel C) or the time that the subject had spent on the standing leg since it hit the ground (Panel D).

Figure 2: Adaptation and Post-adaptation of the parameters S_{out} (targeted) and T_{out} in the spatial feedback and control groups. Left schematics summarize the effect of altering the adaptation of step positions in the adaptation (Panel A) and recalibration (Panel B) of spatial and temporal measures. Stride-by-stride time courses of S_{out} and T_{out} during adaptation and post-adaptation. Each data point in the time courses represents the average of five consecutive strides and shaded areas around the data points represent the standard errors. Bar plots indicate the mean average behavior in the epochs of interest (indicated with the black rectangles), gray dots indicate values for individual subjects, and vertical black lines are standard errors. Lines connecting the bar plots illustrate the significant group by domain interaction, while horizontal lines between bars illustrate significant differences between groups $(p < 0.025)$. **A)** Steady States values of S_{out} and T_{out}: We found a significant group effect and group by domain interaction driven by group differences in S_{out}. **B)** After-effect values of S_{out} and T_{out}: We found a significant group effect and group by domain interaction driven by group differences in S_{out}. Asterisks indicate that after-effect values are significantly different from zero $(p < 0.025)$ according to *post-hoc* analysis.

Figure 3: Adaptation and Post-adaptation for the non-targeted parameters S_A and T_A in the spatial feedback and control groups. Left schematics summarize the effect of altering the adaptation of step positions on the adaptation (Panel A) and recalibration (Panel B) of non-targeted spatial and temporal measures. Stride-by-stride time courses of S_A and T_A during adaptation and post-adaptation. Each data point in the time courses represents the average of five consecutive strides and shaded areas around the data points represent the standard errors. Bar plots indicate the mean average behavior in the epochs of interest (indicated with the black rectangles), the gray dots indicate values for individual subjects, and vertical black lines are standard errors. Lines connecting the bar plots illustrate the significant group by domain interaction, while horizontal lines between bars illustrate significant differences between groups $(p < 0.025)$. **A)** Steady States for S_A and T_A: We found a significant group by domain interaction driven by differences between the spatial feedback and control group in the non-targeted spatial motor output (adaptive motor output). **B)** After-Effects values of S_A and T_A: We found a significant group effect driven by differences in S_A. Asterisks indicate that after-effect values are significantly different from zero $(p < 0.025)$ according to *post-hoc* analysis.

Figure 4: Adaptation and Post-adaptation of the parameters T_{out} (targeted) and S_{out} in the temporal feedback and control groups. Left schematics summarize the effect of altering the adaptation of step times in the adaptation (Panel A) and recalibration (Panel B) of temporal and spatial measures. Stride-by-stride time courses of T_{out} and S_{out} during adaptation and post-adaptation. Each data point in the time courses represents the average of five consecutive strides and shaded areas around the data points represent the standard errors. Bar plots indicate the mean average behavior in the epochs of interest (indicated with the black rectangles), the gray dots indicate values for individual subjects, and vertical black lines are standard errors. Lines connecting the bar plots illustrate the significant group by domain interaction, while horizontal lines between bars illustrate significant differences between groups $(p < 0.025)$. **A)** Steady States values of T_{out} and S_{out}: We found a significant group effect driven by differences between the temporal feedback and control group in the two domains. **B)** After-effect values of T_{out} and S_{out}: We found a significant group effect and group by domain interaction driven by differences between the temporal feedback and control

group in S_{out}. Asterisks indicate that after-effect values are significantly different from zero $(p < 0.025)$ according to *post-hoc* analysis.

Figure 5: Adaptation and Post-adaptation for the non-targeted parameters T_A and S_A in the temporal feedback and control groups. Left schematics summarize the effect of altering the adaptation of step time on the adaptation (Panel A) and recalibration (Panel B) of non-targeted spatial and temporal measures. Stride-by-stride time courses of T_A and S_A during adaptation and post-adaptation. Each data point in the time courses represents the average of five consecutive strides and shaded areas around the data points represent the standard errors. Bar plots indicate the mean average behavior in the epochs of interest (indicated with the black rectangles), the gray dots indicate values for individual subjects, and vertical black lines are standard errors. Lines connecting the bar plots illustrate the significant group by domain interaction, while horizontal lines between bars illustrate significant differences between groups $(p < 0.025)$. **A)** Steady State values of T_A and S_A: We found a significant group effect driven by differences between the temporal feedback and control group in the non-targeted spatial motor output (adaptive motor output). **B)** After-Effects of T_A and S_A: We found a significant group effect and group by domain interaction driven by differences in S_A.Asterisks indicate that after-effect values are significantly different from zero $(p < 0.025)$ according to *post-hoc* analysis.

Figure 6: Adaptation of $T_{!A}$ and $S_{!A}$ measures that were non-targeted parameters in temporal feedback and control group (Panel A) and spatial feedback and control group (Panel B). Left schematics summarize the effect of altering the adaptation of step times or step positions on ”non-adaptive” temporal and spatial measures. Stride-by-stride time courses of $T_{!A}$ and $S_{!A}$ during adaptation. Each data point in the time courses represents the average of five consecutive strides and shaded areas around the data points represent the standard errors. Bar plots indicate the mean average behavior in the epochs of interest (indicated with the black rectangles), the gray dots indicate values for individual subjects, and vertical black lines are standard errors. Lines connecting the bar plots illustrate the significant group by domain interaction, while horizontal lines between bars illustrate significant differences between groups $(p < 0.025)$. **A)** Steady State values of $T_{!A}$ and $S_{!A}$: We found a significant group effect and group by domain interaction driven by differences between the temporal feedback and control group in the non-targeted temporal motor output (adaptive motor output). **B)** Steady State values of $S_{!A}$ and $T_{!A}$: We did not find a significant group effect or group by domain interaction found for the spatial feedback and control group in the parameters of interest.

FIGURES

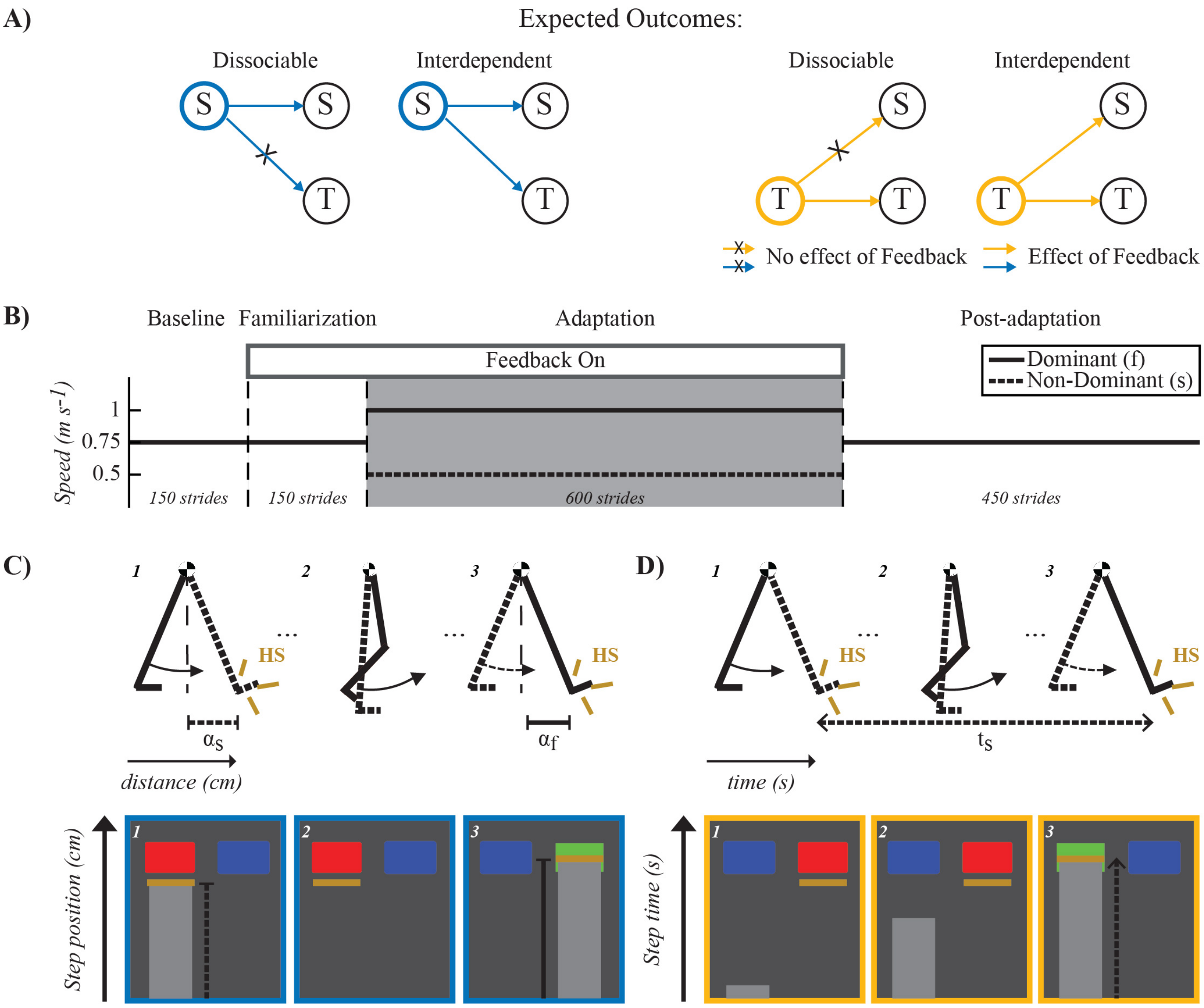
A)
Expected Outcomes:
Dissociable
Interdependent
Dissociable
Interdependent
S
T
No effect of Feedback
Effect of Feedback
B)
Baseline
Familiarization
Adaptation
Post-adaptation
Feedback On
Dominant (f)
Non-Dominant (s)
Speed (m s-1)
1
0.75
0.5
150 strides
150 strides
600 strides
450 strides
C)
D)
1
2
3
HS
αs
αf
ts
distance (cm)
time (s)
Step position (cm)
Step time (s)

Figure 1.

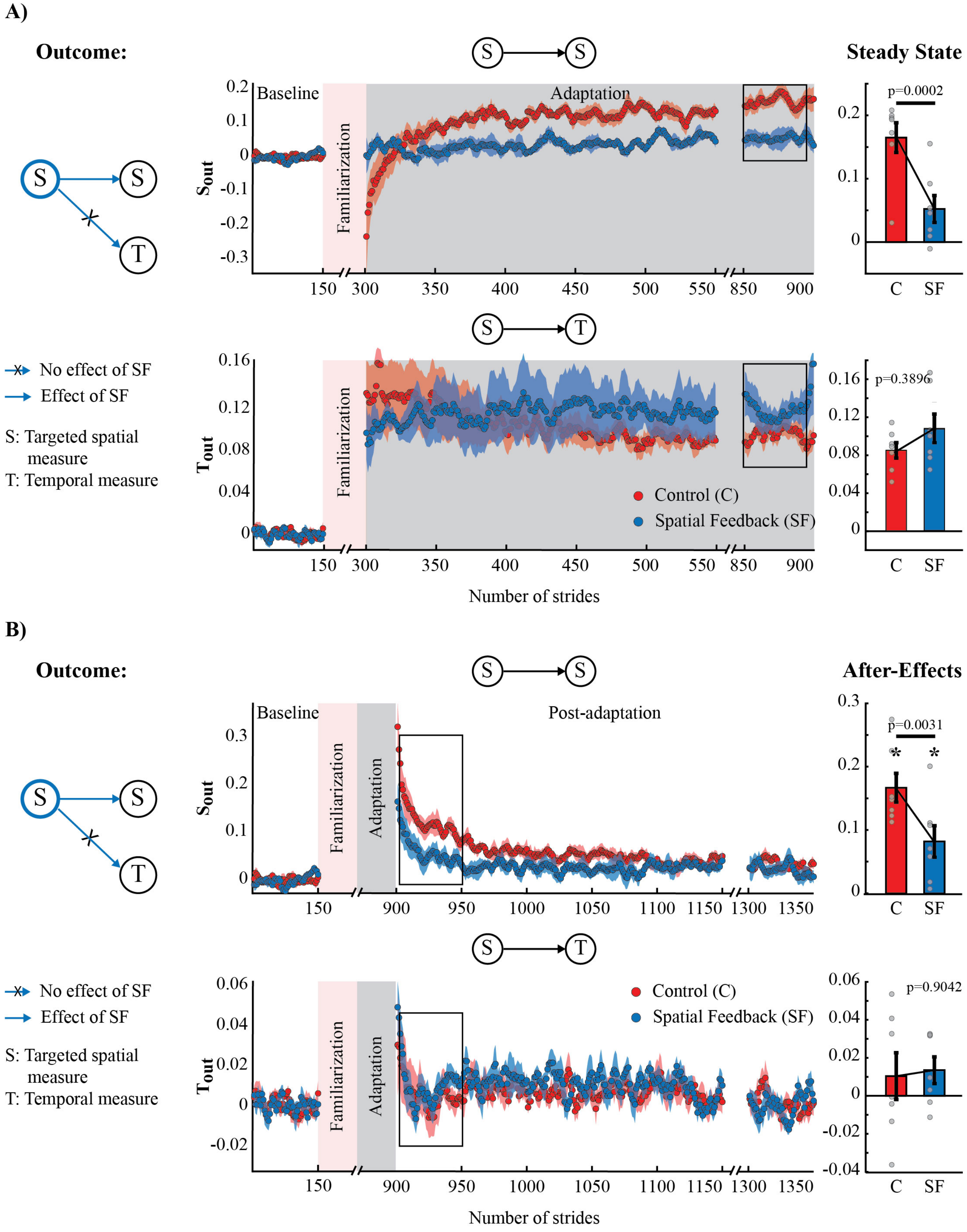
A)
Outcome:
S → S
Steady State
No effect of SF
Effect of SF
S: Targeted spatial measure
T: Temporal measure
Baseline
Familiarization
Adaptation
S_{out}
T_{out}
S → T
p=0.0002
p=0.3896
Control (C)
Spatial Feedback (SF)
C
SF
Number of strides
B)
After-Effects
Post-adaptation
p=0.0031
p=0.9042
*
150
300
350
400
450
500
550
850
900
950
1000
1050
1100
1150
1300
1350

Figure 2.

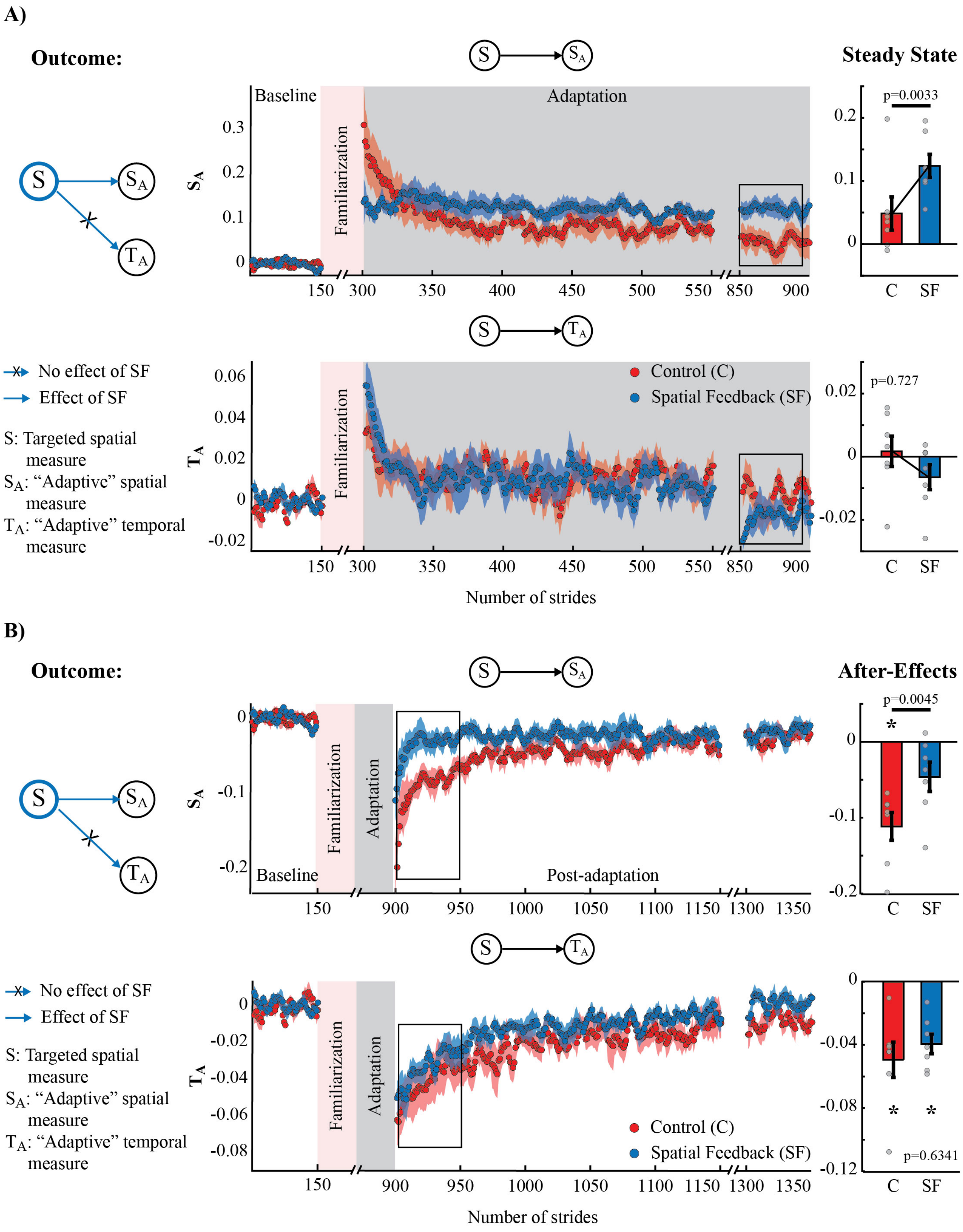
A)
Outcome:
S
S_A
T_A
Steady State
Baseline
Familiarization
Adaptation
S_A
0.3
0.2
0.1
0
150
300
350
400
450
500
550
850
900
p=0.0033
0.2
0.1
0
C
SF
No effect of SF
Effect of SF
S: Targeted spatial measure
S_A: "Adaptive" spatial measure
T_A: "Adaptive" temporal measure
T_A
0.06
0.04
0.02
0
-0.02
Control (C)
Spatial Feedback (SF)
p=0.727
0.02
0
-0.02
Number of strides
B)
Outcome:
After-Effects
p=0.0045
0
-0.1
-0.2
Post-adaptation
900
950
1000
1050
1100
1150
1300
1350
*
-0.02
-0.04
-0.06
-0.08
-0.12
p=0.6341

Figure 3.

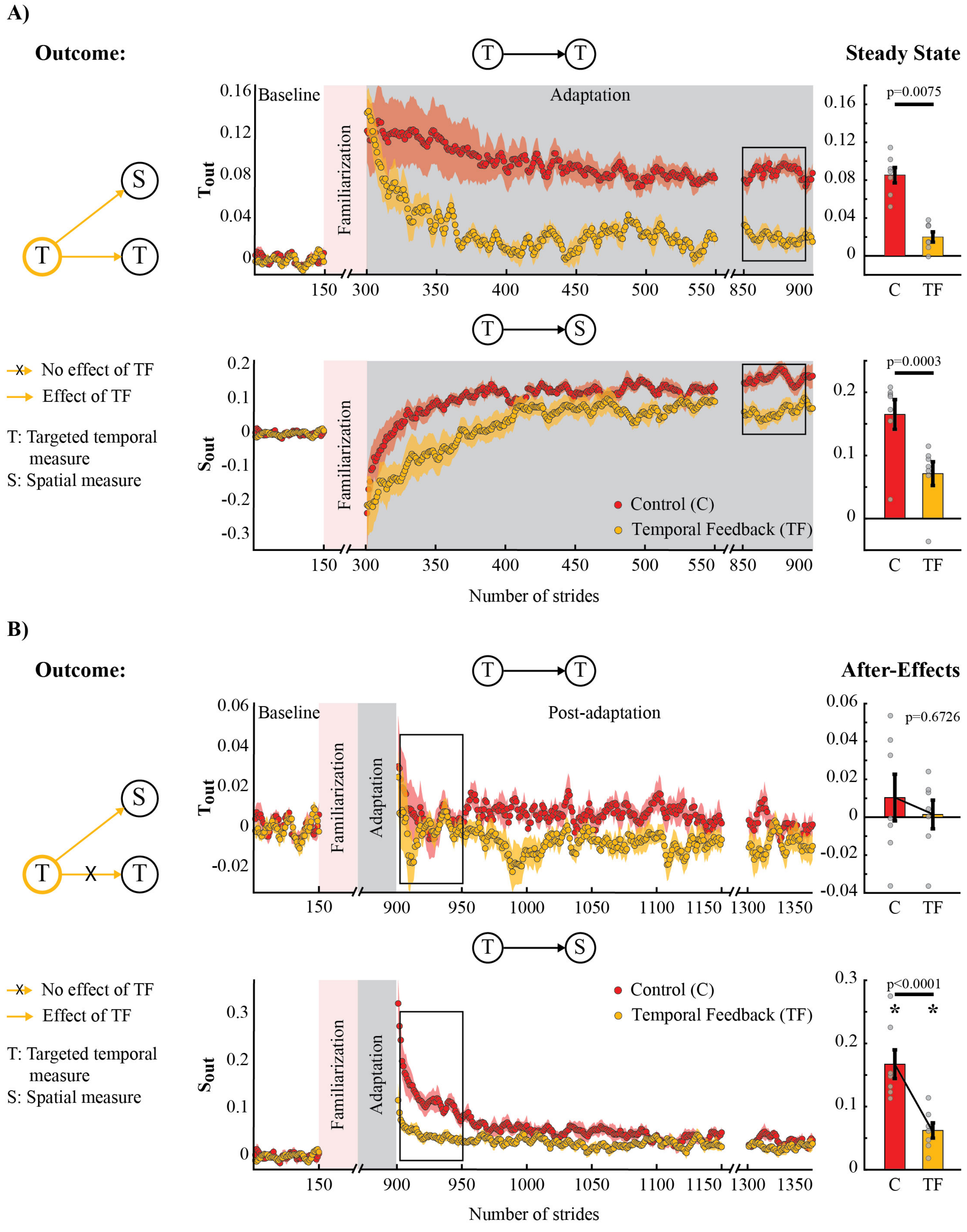
A)
Outcome:
T
S
T
T → T
Steady State
Baseline
Familiarization
Adaptation
Tout
0.16
0.12
0.08
0.04
0
150
300
350
400
450
500
550
850
900
p=0.0075
C
TF
T → S
No effect of TF
Effect of TF
T: Targeted temporal measure
S: Spatial measure
Sout
0.2
0.1
0
-0.1
-0.2
-0.3
Control (C)
Temporal Feedback (TF)
p=0.0003
Number of strides
B)
Outcome:
After-Effects
Post-adaptation
0.06
0.04
0.02
-0.02
-0.04
900
950
1000
1050
1100
1150
1300
1350
p=0.6726
0.3
p<0.0001
*
*

Figure 4.

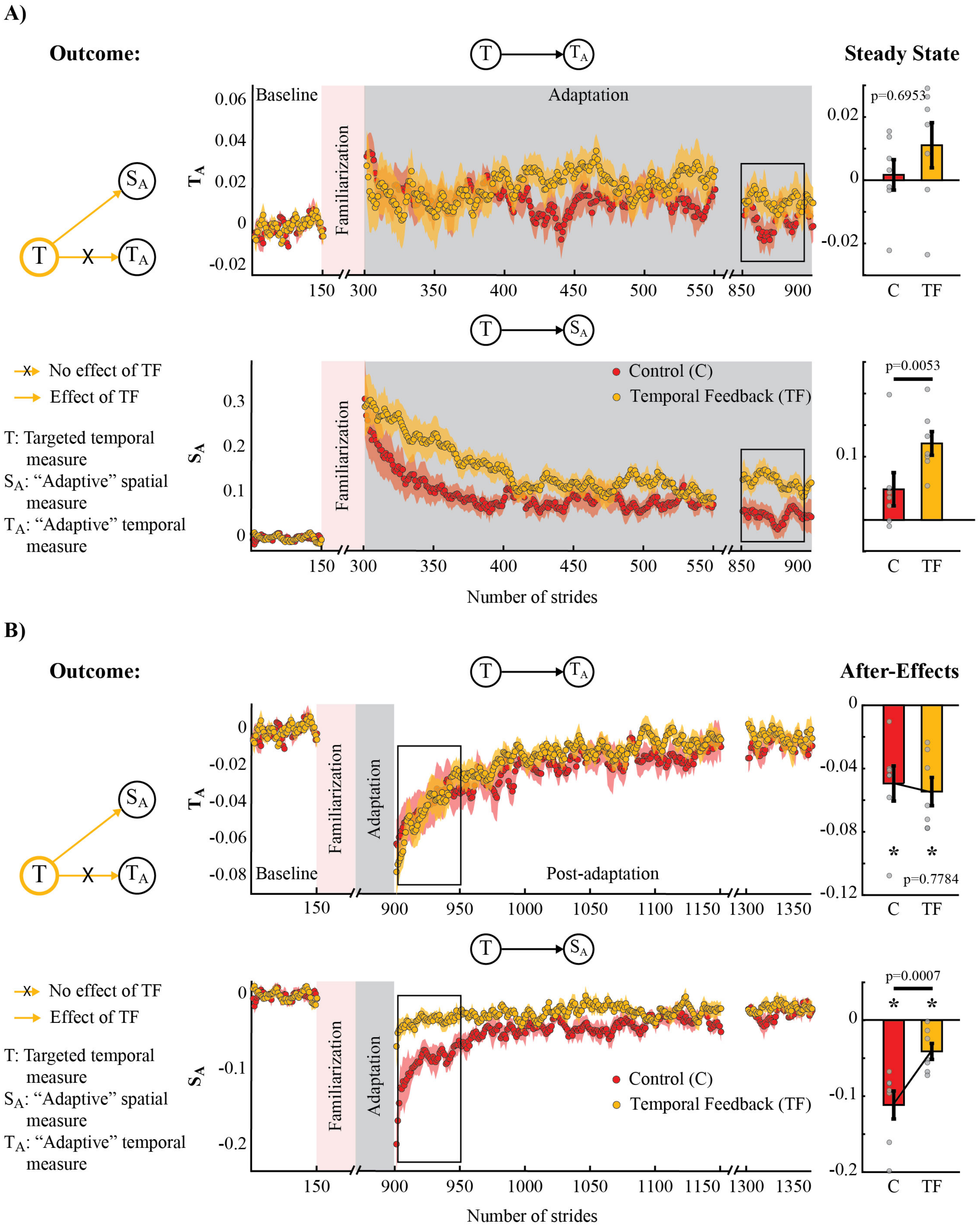
A)
Outcome:
T → T_A
Steady State
T
S_A
T_A
Baseline
Familiarization
Adaptation
T_A
0.06
0.04
0.02
0
-0.02
150
300
350
400
450
500
550
850
900
p=0.6953
0.02
0
-0.02
C
TF
T → S_A
No effect of TF
Effect of TF
T: Targeted temporal measure
S_A: "Adaptive" spatial measure
T_A: "Adaptive" temporal measure
Control (C)
Temporal Feedback (TF)
S_A
0.3
0.2
0.1
0
p=0.0053
0.1
Number of strides
B)
Outcome:
After-Effects
-0.02
-0.04
-0.06
-0.08
Post-adaptation
900
950
1000
1050
1100
1150
1300
1350
-0.04
-0.08
-0.12
*
p=0.7784
-0.1
-0.2
p=0.0007

Figure 5.

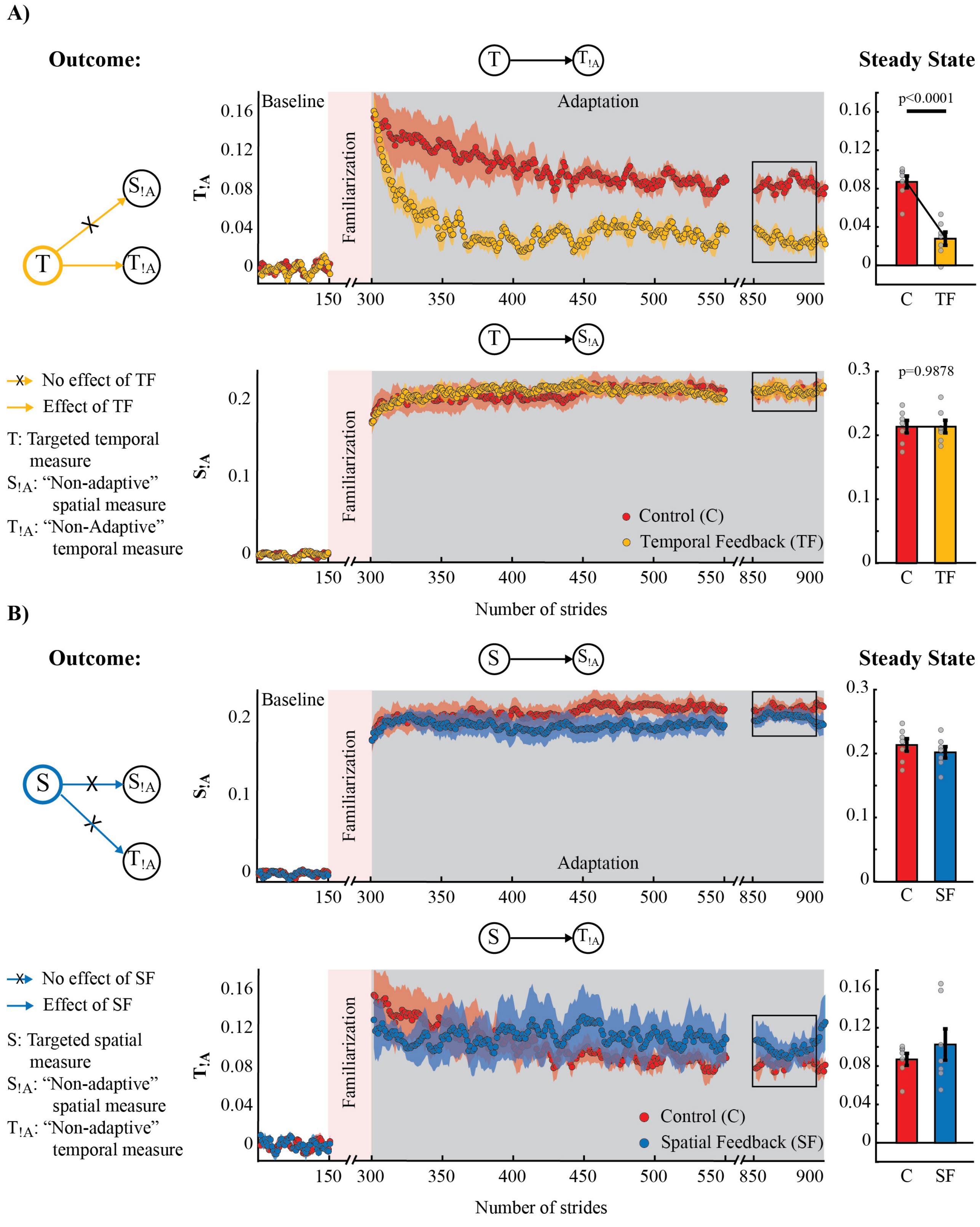
A)
Outcome:
T
$S_{!A}$
$T_{!A}$
No effect of TF
Effect of TF
T: Targeted temporal measure
$S_{!A}$: "Non-adaptive" spatial measure
$T_{!A}$: "Non-Adaptive" temporal measure
T → $T_{!A}$
Baseline
Familiarization
Adaptation
$T_{!A}$
0.16
0.12
0.08
0.04
0
150
300
350
400
450
500
550
850
900
Steady State
p<0.0001
C
TF
T → $S_{!A}$
$S_{!A}$
0.2
0.1
0.3
Control (C)
Temporal Feedback (TF)
p=0.9878
Number of strides
B)
Outcome:
S
No effect of SF
Effect of SF
S: Targeted spatial measure
$S_{!A}$: "Non-adaptive" spatial measure
$T_{!A}$: "Non-adaptive" temporal measure
S → $S_{!A}$
S → $T_{!A}$
Control (C)
Spatial Feedback (SF)
C
SF
Number of strides

Figure 6.