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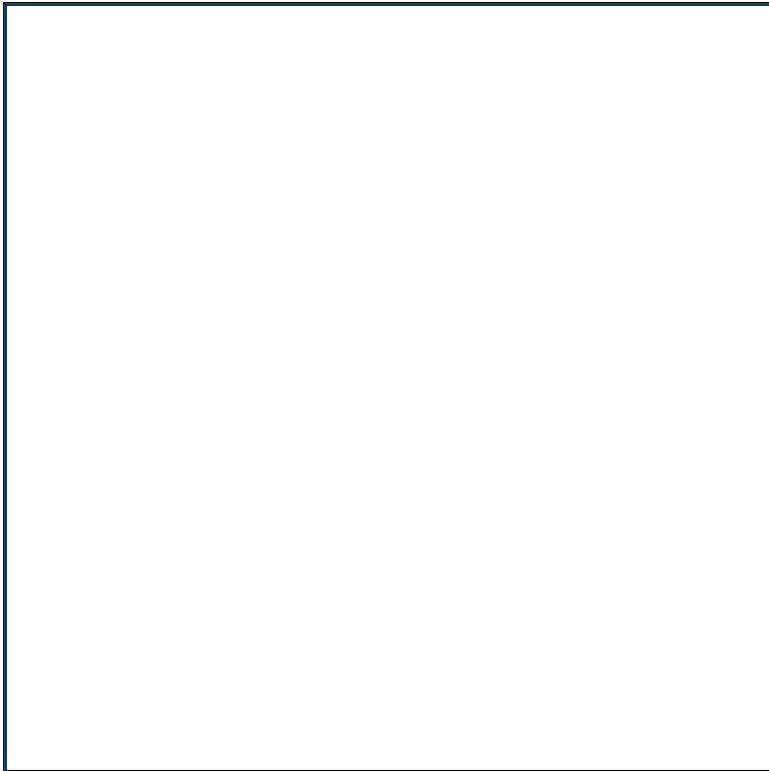
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Tropomyosin Isoforms Specify Functionally Distinct Actin Filament Populations In Vitro

Graphical Abstract



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In Brief

Gateva et al. report that distinct tropomyosin isoforms segregate to different actin filaments and can specify functional properties of distinct actin filament populations. They also provide evidence that functions of tropomyosins in myosin II activation and actin filament stabilization correlate with the dynamics of their actin interactions.

Highlights

- Stress-fiber-associated tropomyosin isoforms segregate to different actin filaments
- Tropomyosin isoforms bind F-actin with different dynamics
- Dynamic tropomyosin isoforms activate non-muscle myosin II
- Stable tropomyosin isoforms protect actin filaments from ADF/cofilin

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Co-authored by Bettina Renz and Hanna Smith, with insights from Tor Bukkvoll, Antulio J. Echevarria, Keir Giles, Sibylle Scheipers, Sir Hew Strachan and Rod Thornton

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modes of warfare, both military (use of force) and non-military (irregular tactics, criminal disorder, terrorist acts, et cetera) to achieve 'synergistic effects in the physical and psychological dimensions' (Hoffman, 2007, p. 8). At the time, 'Hybrid Warfare' was only one of many labels, which also included 'New Wars', fourth-generation warfare and asymmetric warfare amongst others, that were being used by analysts to conceptualise changes in contemporary warfare in line with the idea that war had become 'substantially distinct' (Strachan, 2013, p. 13). After Russia's annexation of Crimea, in which the use of non-military and military means was used as an analytical tool that could help explain Russian military success in this operation. However, in writing about Russia, few analysts have subsequently explicitly used Hoffman's actual concept of 'hybrid warfare' as a conceptual framework of military and non-military means.

It is important to bear in mind that in the context of the history of military-strategic thought, 'hybrid warfare' is only one of many concepts that have seemed to offer a new war-winning formula. A number of prominent examples of such concepts is summarised in the table below. What unites many of these 'war-winning' concepts is that they were constructed, with the expectation that they would be repeatable (e.g. the 'Revolution in Military Affairs' or network-centric warfare based on the success of US coalition operations during the 1991 Gulf War; 'asymmetric warfare' based on the success of Al Qaeda's 9/11 attacks on the US, etc). Proponents of these concepts expected that, what they saw as a 'new' approach to warfare in each case, equated to a war-winning formula that, if captured in doctrine, could guarantee success (e.g. 'strategic bombing' in WWII did not cause targeted populations to turn on their governments, neither in the UK this time, nor in Germany. Technological superiority, precision weapons and a networked approach did not allow the US coalition operations to achieve swift overall and ultimate victory in the 2003 Iraq war, as it had done in the 1991 Gulf campaign).

The idea that any 'new' approach to warfare, including 'hybrid warfare', can lead to repeatable success is a simplification of the complex nature of warfare. It emphasises operational capabilities and doctrine at the expense of strategy. In other words, the presumption that any set mode of warfare or doctrinal approach will lead to military victory irrespective of the circumstances neglects the fact that the success of a strategy is always context-dependent. As Strachan has put it, "Strategy is about doing things, about applying ends to means. It is an attempt to achieve a specific purpose through the use of resources." (Strachan, 2013, p. 13). In other words, presumed 'silver bullets' like 'strategic bombing', 'network-centric warfare' and also 'hybrid warfare' are not a strategy in themselves, but merely means to an end, an operational approach.

3 Frank Hoffman, & Robert A. Hayes, *The Rise of Hybrid Wars*, Arlington, VA: Potomac Institute for Policy Studies, 2007, p. 8.

4 Robert A. Hayes, *The Changing Character of War*, Oxford: Oxford University Press, 2011, pp. 109-10.

5 Hew Strachan, *The Direction of War: Contemporary Strategy in Comparative Perspective*, Cambridge: Cambridge University Press, 2013, p. 13.

LQIRUPDWLRQ WRROV 5XVVLD KDV GHYHORSHG WR VHHN LQÀXHGHFHD
analysed in-depth in Keir Giles' paper prepared for this project.³³ However, as Kofman and Rojansky
also warned, discussing such tools and actions within the framework of 'hybrid warfare' makes it
GLI¿FXOW WR DVVHV V WKHLU µDPELJRXRV DQG RIWHQ LQFKRDWH DL
sian global broadcasting, public diplomacy or propaganda and (military) operational goals. Russian
information warfare can be and has been part of the military operations in Crimea. However, the use
RI LQIRUPDWLRQ WR VHHN LQÀXHGHFHD FDQ DOVR EH DQ HQG LQ LWVH
political outcome.

'Hybrid warfare' as a concept has been useful inasmuch as it highlighted Russia's
strengths in using instruments of state power, such as information, that were not as -
sessed systematically as a security challenge before the Crimea crisis . However, it is
hard to disagree with Kofman and Rojansky, who concluded that 'hybrid war has become a catchall
SKUDVH «UHVXOWLQJ LQ D PLVJXLGHG DWWHPSW WR JURXS HYHU\WK
XQOLNH WKH LGHD WKDW ZH DUH FXUUHQWO\ ZLWQHVV LQJ D µ1HZ &
theory of Russian foreign policy is no more than a very general analogy and as such not useful ei-
ther for scholarly analysis or policy making. As Andrew Monaghan argued such analogies, 'too often
frame[s] the discussion in a repetitive and simplistic polemic that inhibits understanding of Russia
and its relationship with the West. This makes it harder for the West to craft realistic policies with
respect both to the Ukraine crisis and Russia generally'³⁴

33 Keir Giles, 'The next phase of Russian information warfare', unpublished paper prepared for this project.

34 \$QGUHZ 0RQDJKDQ µ\$ ³1HZ &ROG :DU´" \$EXVLQJ KLVWRU\ PLVXQGHU
5HVHDUFK 3DSHU 0D\ S KWWSV ZZZ FKDWKDPKRXVH RUJ VL
¿HOGBGRFXPHQW &ROG:DU5XVVLD0RQDJKDQ SGI!

What are Russian 'national interests'?

7KH ODWHVW 5XVVLQDQ 1DWLRQDO 6HFXULW\ 6WUDWHJ\ SXEOLVKHG 'national interest' to the forefront of Russian goals and intentions once again. However, it is important to note that the concept never really disappeared from Russian rhetoric throughout the post-Cold war period, but in Western analyses its centrality was merely disregarded. One of the reasons for this were Russia's own internal debates during the 1990s, which showed no clear consensus on ZKDW H[DFWO\ FRQVWLWXWHG 5XVVLQDQ QDWLRQDO VHFUXULW\ DQG R or to understand Russian foreign policy through the concept of 'national interests' was too complicated. Russian foreign policy behaviour has continuously puzzled and surprised the West. For example, according to David Mendeloff, Russia did not have an inherently logical reason for backing Milosevic DQG 6HUELQ LQ GXULQJ WKH 1990s. ³⁷ Western analysts have also struggled to assess the balance of material interests versus status/control gains as factors determining Russian international decision-making. ³⁸ Clearly, the fact that Russian foreign policy has often been based on prestige and status rather than on material/economic considerations, has been hard to understand for the West. This is because of the assumption that economics and trade relations matter most in international policy, coupled with an expectation that countries do not act against their own economic interests. This might in fact be one of the biggest Western misperceptions about Russian behaviour and might therefore represent an important root cause of current tensions: Russian behaviour is not all about the economy and economic interests.

Russian Great Power identity and its implications for Russian foreign policy globally, in the post-Soviet region and in Europe

Great Power identity or 'greatpowerness' [derzhavnost] is deeply embedded in Russian strategic culture. As Strachan put it, 'Great Powers of the 19th century, for all that they may QRW EH WKH JUHDW SRZHUV RI WKH WZHQRW\ ¿UVW KDYH QRW ORV VWDXV LQ WKH 20th century have led only to a conclusion that Russia is currently seeking its former Great Power status, that is, that Russia should be categorised as a rising power. This is a misperception and does not correspond to Russia's self-perception of its global status. In fact, both the Russian leadership and public have always regarded their country as a Great Power. In other words, instead of acting like an emerging Great Power, Russia throughout the post-Soviet period has been behaving like a Great Power, or possibly as a declining Great Power struggling to maintain that status. The West's approach to Russia as at best a regional power has created persistent and increasing irritation in Moscow.

When looking for answers to the questions 'what does Russia want?' or 'what are the overarching intentions of Russian foreign policy behaviour?', international recognition of its Great Power

37 'DYLQ 0HQGHORII 3HUQLFLRXV +LVWRU\ DV D &DXVH RI 1DWLRQDO 1999 Kosovo War, & RQÀLFW DQG & RQÀLFW 1R SS ± S

38 3HWHU 6KHUPDQ 7KH VRXUFHV RI 5XVVLQDQ FRQGXFWLQJ RYHU GHUVDQG International Studies , 2001, vol.27, issue 2, pp.249–263.

39 Hew Strachan, Strategy and Limitation of War, Survival, vol.50, no.1, February-March 2008, pp.31–54

for SR and MA from the Russian SOF. The operation was therefore largely CA, most likely based on local agents recruited by the FSB and GRU. Pre-deployment SR by spetsnaz-GRU may have taken observer Dmitrii Tymchuk claims that both FSB and GRU became very active in Ukraine after Viktor Yanukovich became president in 2010. He made the Ukrainian security service SBU change its focus from counterespionage against Russia to counterespionage against the USA. It would also be

Since the operation in terms of SOF was largely CA, it was only to be expected that the newly created SOC would play a crucial role. According to Russian military observers Anton Lavrov and taken by the SOC.¹¹ In particular, SOC was behind the seizing of the local parliament on 27 September. This act made it possible to elect the Russian marionette Sergei Aksenov as new Crimean prime minister. Furthermore, SOC also led the take-over of the Ukrainian military's HQ and a number of other hard-target military compounds. These were all, however, operations that demanded more troops than SOC could provide. The organization was therefore aided by units from spetsnaz-GRU and naval infantry. The SOC, however, was always in the lead.²

The Crimean operation used speed and surprise to establish facts on the ground, thus making transfer of additional troops to the peninsula, but the initial action by SOC and other special and elite forces elements was the decisive element.³ From the take-over of the Crimean parliament to the signing of the treaty making Crimea a part of Russia it took only 19 days. Seven days later all Ukrainian military units had laid down their arms. This time schedule makes the Crimean operation very different from the follow-on operation in Donbas.

Donbas

SOF units. These include all seven spetsnaz GRU brigades, the VDV 45th brigade, and the FSB.¹⁴ An open source, however, seems to claim that the SOC has taken part in these operations. According to

10 'PLWULL 7\PFKXN 3R GHLDWHOQRVWL URVVL Information, 14 April 2014, at <http://sprotyv.info/ru/news/50-po-deyatelnosti-rossiyskih-specslu-zhb-na-vostoke-ukrainy>

11 \$QWRQ /DYURY 35XVVLDQ \$JDLQ 7KH 0LQLOLDU\ 2SHUDWLRQ LQ &ULPWOH *UHHQ DQG 3ROLWH 7KH &UHDWLRQ RI 5XVVLDQ 6SHFLDO 2SHUDARD and Ruslan Pukhov (eds.), 2014, *Brothers Armed – Military Aspects of the Crisis in Ukraine*, Minneapolis, East View Press.

12 Ibid.

13 36SHFLDO IRUFHV' DUH KHUH XQGHUVWRRG DV WKH RQH VLVWHP XQGLXNRY UHIRUPV LQ WKLV VWXG\ 3HOLWH IRUFHV' DUH WKH \$LU ER are elite in the sense that they have a much higher degree of professional soldiers than regular army units, and the selection of personnel is much stricter.

14 See <https://informnapalm.org/12174-russianpresence>

